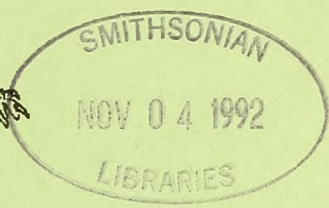
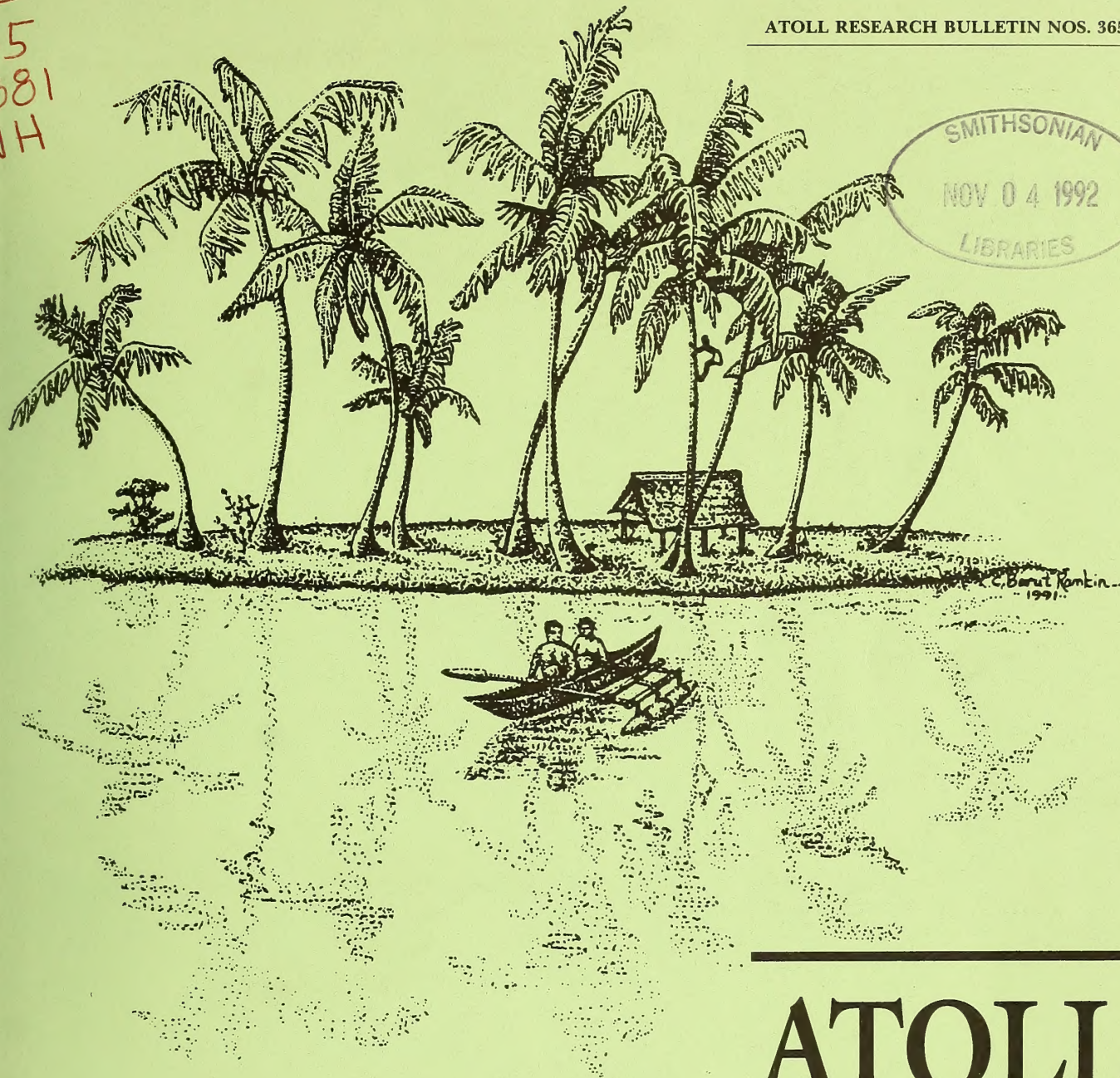


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ATOLL RESEARCH BULLETIN

RESULTS OF THE

USSR-USA EXPEDITION IN MARINE BIOLOGY TO THE
SEYCHELLES ISLANDS

Issued by

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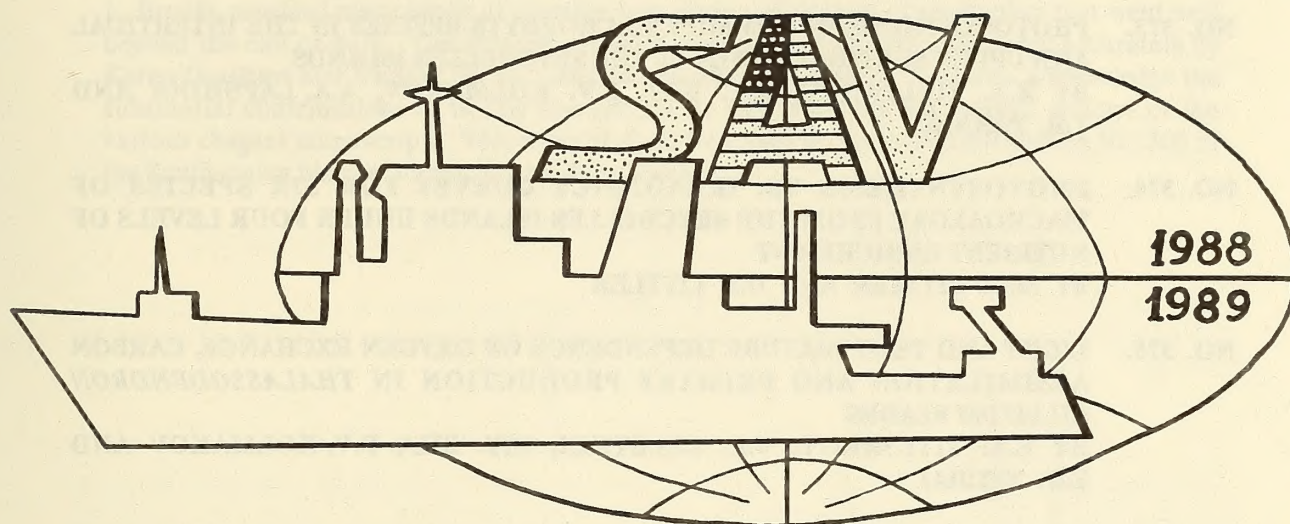
**RESULTS OF THE
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EDITED BY

MARK M. LITTLER AND DIANE S. LITTLER

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- NO. 365. INTRODUCTION TO THE SOVIET-AMERICAN EXPEDITION TO THE SEYCHELLES ISLANDS
BY E.A. TITLYANOV, M.M. LITTLER AND D.S. LITTLER**
- NO. 366. CHARACTERISTICS OF OCEANOGRAPHIC PROCESSES ON REEFS OF THE SEYCHELLES ISLANDS
BY A.V. NOVOZHILOV, Y.N. CHERNOVA, I.A. TSUKUROV, V.A. DENISOV AND L.N. PROPP**
- NO. 367. OCTOCORALLIA FROM THE SEYCHELLES ISLANDS WITH SOME ECOLOGICAL OBSERVATIONS
BY A.N. MALYUTIN**
- NO. 368. SPECIES COMPOSITION AND ABUNDANCE OF CORALS AND OTHER INVERTEBRATES ON THE REEFS OF THE SEYCHELLES ISLANDS
BY N.I. SELIN, Y.Y. LATYPOV, A.N. MALYUTIN AND L.N. BOLSHAKOVA**
- NO. 369. SPECIES COMPOSITION, DISTRIBUTION AND ABUNDANCE OF ALGAE AND SEAGRASSES OF THE SEYCHELLES ISLANDS
BY A.A. KALUGINA-GUTNIK, L.P. PERESTENKO AND T.V. TITLYANOVA**
- NO. 370. FOULING COMMUNITIES OF THE SEYCHELLES ISLANDS
BY A.Y. ZVYAGINTSEV AND V.V. IVIN**
- NO. 371. NITRIFICATION, DENITRIFICATION AND NITROGEN FIXATION IN BOTTOM SEDIMENTS OF LAGOONS OF THE SEYCHELLES ISLANDS
BY M.V. PROPP, V.S. ODINTSOV AND L.N. PROPP**

- NO. 372. NITROGEN FIXING ACTIVITY ASSOCIATED WITH SUBTIDAL MACROPHYTES
OF THE SEYCHELLES ISLANDS
BY V.S. ODINTSOV
- NO. 373. PHOTOSYNTHESIS IN COMMON MACROPHYTE SPECIES IN THE INTERTIDAL
AND UPPER SUBTIDAL ZONES OF THE SEYCHELLES ISLANDS
BY E.A. TITLYANOV, K.Y. BIL', P.V. KOLMAKOV, A.A. LAPSHINA AND
T.R. PÄRNIK
- NO. 374. PHOTOSYNTHESIS VS. IRRADIANCE CURVES FOR SIX SPECIES OF
MACROALGAE FROM THE SEYCHELLES ISLANDS UNDER FOUR LEVELS OF
NUTRIENT ENRICHMENT
BY M.M. LITTLER AND D.S. LITTLER
- NO. 375. LIGHT AND TEMPERATURE DEPENDENCE OF OXYGEN EXCHANGE, CARBON
ASSIMILATION AND PRIMARY PRODUCTION IN *THALASSODENDRON*
CILIATUM BLADES
BY E.A. TITLYANOV, V.A. LELETKIN, K.Y. BIL', P.V. KOLMAKOV AND
E.G. NECHAI
- NO. 376. PHOTOSYNTHESIS OF THE SEAGRASS *THALASSODENDRON CILIATUM*: LEAF
MORPHOLOGY AND CARBON METABOLISM
BY T.R. PÄRNIK, K.Y. BIL', P.V. KOLMAKOV AND E.A. TITLYANOV
- NO. 377. PHOTOSYNTHETIC PRODUCTS OF ZOOXANTHELLAE OF THE REEF-
BUILDING CORALS *STYLOPHORA PISTILLATA* AND *SERIATOPORA*
COLIENDRUM
BY K.Y. BIL', P.V. KOLMAKOV AND L. MUSCATINE
- NO. 378. ESTIMATES OF INDIAN OCEAN PRODUCTIVITY USING NATURAL
FLUORESCENCE
BY P. DUSTAN

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Articles submitted for publication in the Atoll Research Bulletin should be original papers in a format similar to that found in recent issues of the Bulletin. First drafts of manuscripts should be typewritten double spaced. After the manuscript has been reviewed and accepted, the author will be provided with a page format with which to prepare a single-spaced camera-ready copy of the manuscript.

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**ATOLL RESEARCH BULLETIN
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CHAPTER 1
INTRODUCTION TO THE SOVIET-AMERICAN EXPEDITION
TO THE SEYCHELLES ISLANDS
BY
E. A. TITLYANOV, M. M. LITTLER AND D. S. LITTLER

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CHAPTER 1
INTRODUCTION TO THE SOVIET-AMERICAN EXPEDITION
TO THE SEYCHELLES ISLANDS

BY

E.A. Titlyanov^{*}, M.M. Littler^{} and D.S. Littler^{**}**

BACKGROUND AND OBJECTIVES

The First Soviet-American Expedition in Marine Biology to the Seychelles Islands was organized by the Institute of Marine Biology, Far East Branch of the USSR Academy of Sciences, at the request of the Seychelles Government. The Republic of the Seychelles Islands sought information on the marine plant resources and productivity of benthic and planktonic communities of the Seychelles Bank. After discussing the program of work in the Department of Development of the Republic of the Seychelles Islands with the Deputy Minister, Mr. Selvine Jandron, the following research objectives were established for the expedition:

- 1) To study the benthic marine biota and fouling processes of the Seychelles Islands, which represents a poorly investigated region of the Indian Ocean.
- 2) To provide the first analyses of the species composition of algal communities for several remote island groups (Farquhar Atoll, Coëtivy Atoll, Cosmoledo Atoll, Amirantes Group) and to supplement previous knowledge on the algae of Aldabra Atoll, Mahé Island and Praslin Island.
- 3) To study the distribution of autotrophic organisms over the various reef systems and determine the depth ranges of algae, seagrasses and corals.
- 4) To evaluate the common algal and seagrass resources in the area of study, particularly species of commercial interest.
- 5) To estimate the production potential of the major producers of organic matter on Seychelles reefs; i.e., benthic macroalgae, seagrasses, reef building corals and phytoplankton.
- 6) To assess the prevalent environmental parameters of the various island groups studied: e.g., optical characteristics of the water, seawater temperatures, nutrient contents, oxygen levels, pH and current velocities.
- 7) To investigate the adaptations of photosynthetic organisms to light, nutrients, temperature and water motion.
- 8) To study nitrogen and phosphorus metabolism in macrophytes and nitrogen cycling in bottom sediments on island coasts, lagoons, channels and reef-flats.

Proceeding from the above objectives, the First USSR-USA Expedition in Marine Biology to the Seychelles Islands was complex with 62 specialists from various disciplines

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participating: 55 from the USSR, 6 from the USA and 1 from Vietnam. The expedition had its own logo (see cover page) with the letters "SAV," which suggested the international character of the expedition: Soviet-American-Vietnamese.

The expedition took place aboard the R/V Akademik A. Nesmeyanov from 14 December 1988 to 11 April 1989. The route of the expedition was as follows (Fig. 1): the ship departed Vladivostok 14 December 1988 and via Singapore arrived at the Port of Victoria 9 January 1989. The research on the Seychelles Islands was conducted from 9 January 1989 to 16 March 1989. From 17 March 1989 to 11 April 1989, the expedition transited back to Vladivostok (again via Singapore). Altogether, the expedition examined 11 Seychelles island groups, including the Amirantes Group, Cœtivy Atoll, Farquhar Atoll, Aldabra Atoll, Astove Atoll, Cosmoledo Atoll, Providence, Mahé, Praslin, La Digue, Desroches, African Banks and St. Joseph Atoll.

PARTICIPANTS

The administrative members of the expedition included the following: the Head of the Expedition - Prof. E.A. Titlyanov, marine algal and coral physiologist; the Assistant Science Heads - Dr. Y.Y. Latypov, coral taxonomist and ecologist, and Dr. P.V. Kolmakov, specialist in carbon metabolism of algae; the Assistant Head of Transport - Captain Oleynik S.D.; the Scientific Secretary of the expedition - Dr. T.A. Terekhova, specialist in lipid metabolism of marine organisms.

The expedition was organized into the following research groups:

- 1) The Taxonomic Group (under the direction of Dr. A. Kalugina-Gutnik from the Institute of South Seas Biology, Sevastopol), which conducted taxonomic and biocoenological studies of algae and seagrasses;
- 2) The Biological Communities Group (led by Dr. Y.Y. Latypov and Dr. N.I. Selin, Institute of Marine Biology, Far East Branch, USSR Academy of Sciences, Vladivostok), which assessed vertical and horizontal distributional patterns;
- 3) The Productivity Group (Dr. M.V. Propp, Institute of Marine Biology), which evaluated primary production of plankton and studied nitrification processes in sediments;
- 4) The Algal and Coral Physiology Group (Prof. E.A. Titlyanov, Institute of Marine Biology), which investigated light and temperature dependence of photosynthesis in algae, seagrasses and reef-building corals, including adaptations of plants to major environmental factors;
- 5) The Radioisotope Group (Dr. K.Y. Bil', Institute of Soil and Photosynthesis, USSR Academy of Sciences, Puschino, Moscow), which studied potential photosynthetic capacities of autotrophic plants, their apparent photosynthesis under natural conditions and mechanisms of carbon metabolism;
- 6) The Hydrology Group (Dr. A.V. Novozhilov, Institute of Marine Biology, and Dr. E.A. Chernova, Pacific Institute of Geography, Far East Branch), which investigated currents, turbulence, temperature and transparency of waters at different depths and estimated major biogenic elements and metals in seawater;
- 7) The Biochemistry Group (Dr. N.A. Latyshev), which estimated the content of biologically active lipids in marine algae and soft corals.

The American scientists included: Andrew Benson, Member of the U.S. National Academy of Sciences, Scripps Institution of Oceanography, La Jolla, specialist in carbon reduction metabolism and arsenic metabolism in plants; the group from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. - Mark Littler, Senior Scientist, physiology and ecology of marine algae; Diane Littler, Research Associate, taxonomy and ecology of algae; Barrett Brooks, Scientific Assistant; Leonard Muscatine from the University of California, Los Angeles, physiology

and cell biology of reef-building corals, and Phillip Dustan from the College of Charleston, specialist in coral adaptation to light.

Dr. Pham Van Huen from the Institute of Marine Research, SRV, Nhatrang, specialist in hydrochemistry of tropical waters, also participated in the expedition. In order to fulfill the goals of the extensive research program, the following specialists were included in the expedition as well: Dr. L.P. Perestenko, Institute of Botany, Leningrad, algal taxonomist; Prof. V.M. Gol'd, University of Krasnoyarsk, specialist in productivity of phytoplankton; Dr. T.R. Pärnik, Institute of Experimental Biology, Estonia, specialist in photosynthesis. The Chief Dive Officer was Y.P. Popov, a diver of USSR 1st class status. The Master of the ship was A.V. Gulyaev, a certified long voyage captain. Altogether, there were 62 scientists and 60 crew members aboard the R/V Akademik A. Nesmeyanov.

PRELIMINARY FINDINGS

During the expedition, the ship transited a total of 17,163 nautical miles. Out of a total of 116 days, research was conducted on station during 41 days, transitions took a total of 61 days, mooring at ports (Singapore, Victoria, Mombasa) required 14 days. The expedition studied 12 island groups of the Seychelles including Cœtivy Atoll, Farquhar Atoll, Aldabra Atoll, Desroches, Praslin, Mahé, La Digue, African Banks, St. Joseph Atoll, Providence, Cosmoledo Atoll and Astove Atoll. A total of 257 benthic stations were studied, 687 samples of phyto-benthos were collected and analyzed, 479 of these were quantitative. The macrophytic standing stocks of 28 intertidal and 37 subtidal transects were assessed at depths ranging from 0 to 50 m. All hydrobiological and benthic investigations were carried out by snorkling and SCUBA diving. The first results of these investigations are presented in the following collection of works. This introductory chapter provides a general overview and highlights some of the main findings.

The total list of plants collected includes 8 seagrass species and 292 algal species (161 Rhodophyta, 92 Chlorophyta, 30 Phaeophyta and 9 Cyanophyta). Algae were most diverse and abundant on the high granitic islands of Mahé and Praslin, where 168 and 114 species, respectively, were collected (see Figs. 2-8). The high granitic islands (Mahé, Praslin and La Digue) also were rich in macroalgal communities dominated by *Sargassum* (Phaeophyta, Figs. 6 and 7), with fresh weight biomass ranging up to $8-10 \text{ kg}\cdot\text{m}^{-2}$. Agar containing algae, chiefly *Gracilaria crassa*, with a biomass of up to $3-6 \text{ kg}\cdot\text{m}^{-2}$, were also prominent on high islands (Fig. 8).

The species composition of algae on low calcareous islands was not as rich and ranged from 40 (Providence Group) to 119 (Aldabra Atoll) species per island group. In the floras of low carbonate islands, species of Rhodophyta (52-62%) and Chlorophyta (22-44%) predominated, whereas Phaeophyta were few (2-7%).

The marine vegetation of carbonate islands is dominated mainly by phytocoenoses of abundant seagrasses, with *Thalassodendron ciliatum* as the main community- (coenosis) forming species. Biomass estimates of seagrasses and algae of coral islands varied from 0.5 to $3.5 \text{ wet kg}\cdot\text{m}^{-2}$. According to expedition estimates, the marine plant stocks of Cœtivy, Farquhar and Desroches comprise 1,963,000, 195,100 and 16,600 tons of fresh mass, respectively. One hectare at Cœtivy contains, on average, 15 tons of fresh mass, compared with 19 t at Farquhar and 23 t at Desroches.

Collections of Octocorallia made on the expedition nearly doubled the published list of species known for the Seychelles Islands.

The species composition and distribution of corals, mollusks and sponges was investigated

throughout intertidal and upper subtidal zones for 12 of the Seychelles island groups. The data obtained substantially increased the available knowledge of the biology of reef systems of this region and will be useful in planning fishery, mariculture and tourism activities.

The composition, distribution and patterns of fouling on ships and hydrotechnical constructions were investigated and described near Mahé, Farquhar, Aldabra, Desroches and Praslin islands. The physical removal of fouling communities in the tropical waters of the Seychelles often led to very rapid refouling that was more extensive than the previous communities.

Using a fluorescence system of diagnosis, physiological and production characteristics of phytoplankton were studied at 52 shelf and 12 oceanic stations. Based on the data obtained, total phytoplankton production of the Seychelles Bank was evaluated.

Patterns of changes of nitrogen content were determined, which proved to be a major limiting element in sediments of the Seychelles. Considerable differences in the processes of nitrogen transformation were shown in sediments of high granitic islands (Figs. 2-8) versus low carbonate atolls (see Figs. 9-15), that are related to different concentrations of iron.

Light and temperature dependence of photosynthesis, pigment composition, morphology, anatomy and paths of photosynthetic carbon metabolism were studied in seagrasses, macroalgae and corals in reference to environmental conditions. It was shown that the seagrasses, macroalgal species and coral zooxanthellae investigated have characteristic C_3 -photosynthesis. Macrophytic algae of the Seychelles Islands show a relatively great capacity for photosynthetic apparatus acclimation, but tend to have comparatively low levels of photosynthesis.

The intensity of photosynthesis and respiration was measured in respect to the exchange of nitrogen, phosphorus and dissolved organic matter in species of corals, algae, seagrasses and periphyton in reference to ecological factors in the region of study. The dependence between the intensity of photosynthetically active radiation, fluctuations in the content of biogenic elements and production efficiency of the reef ecosystem was documented. Some of the mutualistic interactions as well as nontrophic interactions between the more common species of animals and plants in the area were defined.

GEOLOGICAL HISTORY

As pointed out by Stoddart (1984a), the Seychelles are unique among the world's isolated islands in that some of them are of continental origin. The granitic group of islands (Mahé, Praslin, La Digue) are about 650 million years old and constitute a 'micro-continent' isolated by continental drift during the formation of the Indian Ocean. Thus, the granitic islands are biogeographically interesting in that they would be predicted to contain elements of a much older biota with links to India and Madagascar.

The low carbonate islands may be as old as the Eocene, having been built on now subsided volcanoes (Stoddart 1984a). All have been greatly modified by Pleistocene fluctuations in sea level and as a result their biotas are likely to be derived mainly by processes of long-distance dispersal.

MARINE BIOLOGICAL STUDIES

The 1964 International Indian Ocean Expedition provided the geological groundwork for future detailed studies of Seychelles reefs (Stoddart 1984a). The Sealark Expedition of 1899-1900 produced

early inventory information, with about 120 macroalgal species collected by J. Stanley Gardiner (Gepp and Gepp 1908, Weber van Bosse 1913). More recently, Titlyanova and Butorin (1978) doubled the known records of macrophyte species from Mahé and Cœtivy Islands, and Aleem (1984) described the seagrass communities of Mahé, Latam, Aldabra, Comoro, Farquhar and Amirantes Islands. Especially noteworthy are the studies conducted through the Royal Society of London Research Station on Aldabra, which have been reviewed by Stoddart (1967, 1970). Price (1971) also reported on the sublittoral ecology of Aldabra, while Taylor (1968) and Taylor and Lewis (1970) treated some of the reef and seagrass invertebrate communities around Mahé. Research on Seychelles and other western Indian Ocean reefs has been reviewed by Stoddart and Young (1970). Further specialized inventory studies on the marine biota have focused on Aldabra Atoll and are included in a special volume of the Bulletin of the Biological Society of Washington, edited by Kensley (1988). Despite their long history, biological knowledge of the reefs of the Seychelles remains at the inventory level. This lack of both synoptic and detailed information led us to turn our attention to the marine primary producers of this unusual island group.

CLIMATIC CONDITIONS

The Seychelles Islands are situated in the subequatorial climatic zone, which is characterized by a predominance of the equatorial air mass in summer (December-March) and different air masses in winter (June-September). Seasonal changes of wind direction occur with summer winds blowing from the equator (northwestern monsoon), whereas in winter, winds blow towards the equator (southeastern trade wind). Summers are humid and rainy, with unsteady winds and thunderstorms. Wind directions are as follows: from January to March - northwestern monsoon, recurrence 30-50%; from May to November - southeastern monsoon, recurrence 50-85%; from April to December, winds are unsteady, average monthly wind velocities are $2-6 \text{ m}\cdot\text{sec}^{-1}$ throughout most of the subequatorial zone.

Increased rainfall and terrigenous runoff due to greater adiabatic cooling of monsoonal winds on the rainforested high granitic islands (Procter 1984; Walsh 1984) should result in an increase in organically-derived nutrient availability (Littler et al. 1992) in nearshore waters. Nutrient input into low island systems is mainly from normal oceanic water throughput, presumed episodic upwelling and nitrogen fixation. Some of the low carbonate islands receive considerable enrichment from terrestrial erosion of both modern and fossil guano deposits. Winter is somewhat cooler than summer, less rainy, with steady moderate winds. The average monthly humidity is more than 70% in the hottest period of the year (December-April) when air temperatures reach $26-29^{\circ}\text{C}$.

Average monthly cloud cover in the open ocean and on islands varies from 3 to 7 percent within a year, recurrence of clear sky conditions ranges from 10 to 30% within a year, however from May to November in the western region of the zone it increases to 40-60%. On high islands, the average monthly number of clear days during the year is 1-3, the total yearly amount of precipitation is 1500-2700 mm and, on the windward slopes of high granitic islands, rainfall may exceed 3000-3500 mm. The greatest amount of precipitation occurs from December to March, 183-482 mm per month, and the number of rainy days varies from 11 to 22 during each month.

The hydrological regime of the Seychelles Islands is characterized by high water temperatures with small seasonal and yearly fluctuations ($27-31^{\circ}\text{C}$), a predominance of waves 1-2 m in height, a salinity range of 34.5 to 35.5‰, small fluctuations in tidal level and well-developed systems of constant currents (Taylor and Lewis 1970). Inter-trade wind countercurrent conditions, observed from November to March between approximately 3° and 8° S and running from west to east with an average rate of 0.5 knots and stability of 25-50%, play an important role in the formation of the dominant current regime of the area.

GEOMORPHIC CHARACTERISTICS

The detailed geomorphology of Seychelles island groups, including all those visited by the expedition, has been characterized in Stoddart (1984b). The Seychelles Islands and Seychelles-Mascarene depression represent a micro-continent, which was formed from the ancient continent Gondwana about 130 million years ago (Johnson et al. 1976). According to their geomorphology, the islands are subdivided into high granitic groups (e.g., Mahé and Praslin, Figs. 2-5), low calcareous groups (e.g., Desroches and Alfons) and slightly higher carbonate groups (e.g., Aldabra, Cosmoledo and Astove, Figs. 9-12). Granitic islands are formed of gneiss granites (Figs. 2-4), have steep shores and, as a rule, are fringed with shallow borders of carbonate sand (Figs. 5 and 6). Low calcareous islands do not rise more than 2-3 m above sea level (Fig. 12) and are composed of bioplastic sand and coral rubble (Fig. 11) transported from reef-flats by storms. Deposits of phosphorites are observed on some low islands (described as "guano," Baker 1963, Fig. 12). Higher limestone islands rise up to 8 m above sea level (Fig. 9). Aldabra, Cosmoledo and Astove are atolls with a well-developed central lagoon.

In the example of Aldabra Atoll, three types of geomorphological forms of relief are present, which are connected with their lithological features and external erosive processes (Stoddart 1984, Braithwaite 1984). Intensive aerial decay and washing away of reef surfaces have led to formation of a specific surface with highly irregular sharp edges and knife-like projections (Fig. 10), the so-called champignon surface. Other surficial forms (e.g., plain, smooth, hard surfaces) were probably formed from the bottom of ancient lagoons. The third type of relief, called pavement, may have been formed from submarine erosion of ancient reefs.

Modern reef formation is closely connected with the geological history of the various islands, their geomorphology and ongoing erosive processes, which determine the conditions of present sedimentation. There are three kinds of reefs in the Seychelles islands: fringing, platform and atolls (Stoddart, 1984b). Fringing reefs (Figs. 5 and 6) are formed on the coastlines of the granitic islands of the Seychelles Bank and are most extensive on Mahé and Praslin islands. These reefs extend as uneven belts from 500-750 m in width along the southeastern coast of Mahé, whereas along Mahé's northwestern coasts these belts reach 1500 m in width and have deep (up to 15 m) transverse channels. The degree of irregularity and jaggedness of reefs are connected with the erosive history of pleistocene reefs and the absence of strong wave action (Lewis, 1969). At Praslin, the fringing reef reaches more than 2850 m in width (Fig. 6), although in the most narrow places it is only 380 m wide. The high islands occur on a granitic base where blocks of reef rock rising up to 9 m above sea level (Figs. 2-4) consist of fragments of granite combined with carbonate shells, coral rubble, coral sand and remains of calcareous algae.

Platform reefs are found on some of the low islands (not more than 2-3 m in height above sea level) and are formed by calcareous detritus deposits transported from reef flats (Figs. 10 and 11). Such reefs can extend over large or small portions of an island system (Côtevivy - 37%, Desroches - 68%, Providence - 20%).

The atolls of the Seychelles usually include a number of islands of various sizes forming an irregular ring with several passages into a shallow central lagoon (Fig. 9). The largest lagoon occurs at Farquhar Atoll (14.6 km diam). As a rule, lagoons have underwater deltas, channels and inner breakwaters (edge or crest of a reef) formed by karst erosion of an ancient reef. The width of "rings" of atoll reefs ranges from 80 to 3250 m. The outer windward margins are usually wider than the leeward borders. Atolls of Aldabra, Cosmoledo and Astove are formed on elevated ancient reefs. The shallow lagoons of such reefs are infilled with sand, silts and stony coral deposits. Living corals (Figs. 13 and 14) reach their maximal development in the channels at the outlets of lagoons. The

outer reef intertidal zones are represented by stony benches and platform regions of old reefs. The subtidal zones are formed by erosive halcyon reef coral deposits and the slopes are made up of coral and *Halimeda* sands, often dominated by the seagrass *Thalassodendron ciliatum* (Fig. 15).

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Fig. 1. Cruise Track of the USSR-USA Expedition in Marine Biology. Large blocked area indicates Seychelles granitic islands, small blocks indicate calcareous island groups.



Fig. 2. Praslin Island showing the high topography and coastal granitic rock formations.



Fig. 3. Mahé Island showing the high topography and coastal granitic rock containing intertidal *Sargassum* communities.



Fig. 4. Granitic boulder on Mahé characteristic of Seychelles high islands.



Fig. 5. Fringing reef on Mahé Island dominated by macroalgal communities.



Fig. 6. Fringing reef on Praslin Island showing the expedition's intertidal taxonomic group approaching dark *Sargassum* communities toward the shoreline.



Fig. 7. Subtidal fringing reef macroalgal community dominated by the brown rockweeds *Sargassum* and *Turbinaria* characteristic of Seychelles high granitic islands.



Fig. 8. Intertidal community near Victoria Harbor, Mahé, dominated by large heads of the red alga *Gracilaria* growing on rubble.



Fig. 9. The outer reef platform of Astove Atoll showing seawater transport from the lagoon passage at low tide.



Fig. 10. Elevated and highly eroded fossil carbonate reef relief adjacent to the lagoon passage of Astove Atoll.

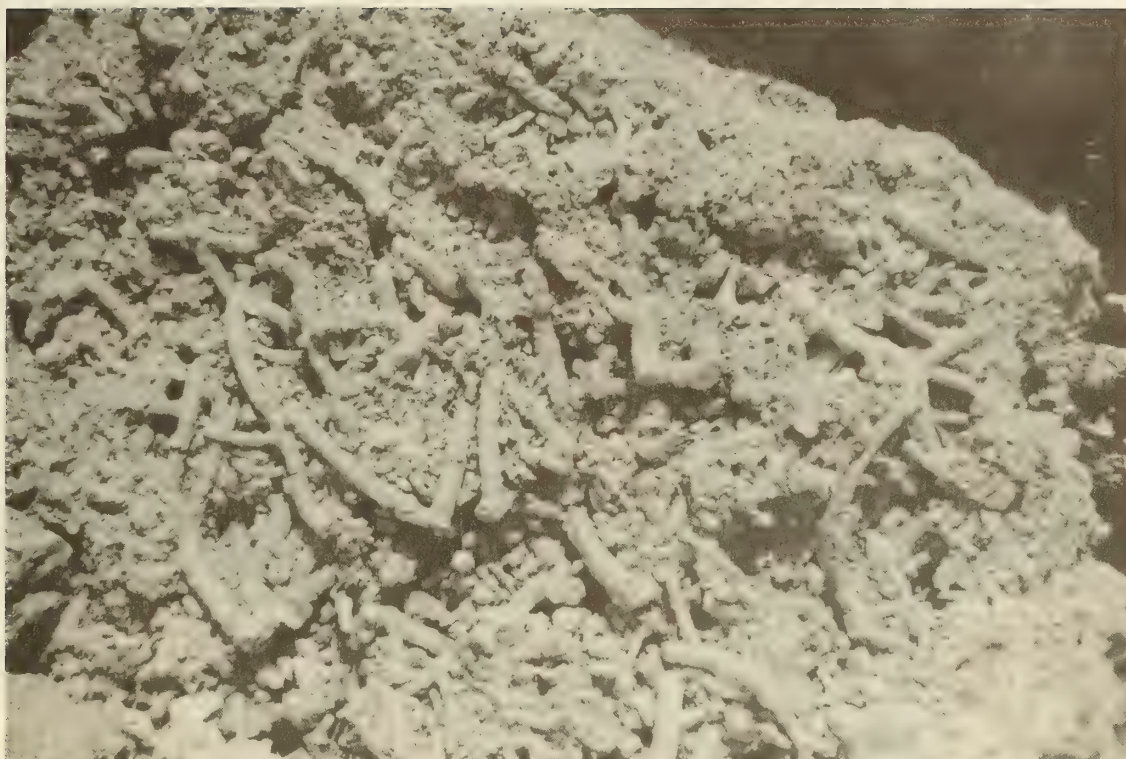


Fig. 11. Fragment of carbonate island substrate showing consolidated coral fragments and sediments.



Fig. 12. Pagode Island of the Cosmoledo Group with extensive guano build-up due to seabird rookeries.

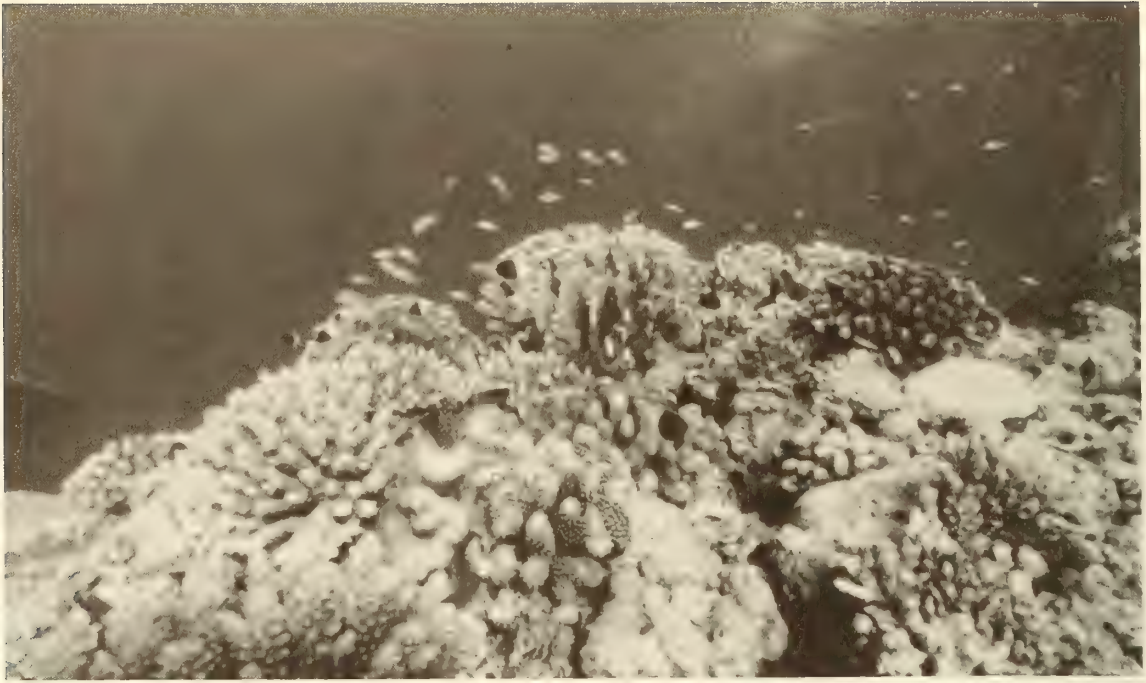


Fig. 13. Hermatypic coral community typical of Seychelles low carbonate islands (Cosmoledo Atoll).



Fig. 14. Alcyonarian and stoney coral community characteristic of low carbonate atolls (Cœtivy Atoll).



Fig. 15. Subtidal *Thalassodendron ciliatum* characteristic of Seychelles soft-bottom habitats (25 m deep, African Banks).



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**CHAPTER 2
CHARACTERISTICS OF OCEANOGRAPHIC PROCESSES ON REEFS
OF THE SEYCHELLES ISLANDS**

**BY
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CHAPTER 2

CHARACTERISTICS OF OCEANOGRAPHIC PROCESSES ON REEFS OF THE SEYCHELLES ISLANDS

BY

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INTRODUCTION

Tropical reef ecosystems are formed under conditions of complex variability of physical-chemical environmental factors. The shape of coral reefs depends to a great extent on the pattern of surface currents (Brown and Dunne 1980). Underwater geomorphological features of reef slopes and plateaus (buttress and reef-flat systems) abounding in spurs, coral columns, hollows, channels and tunnels are primarily the result of abrasive wave forces (Munk and Sargent 1954, Storr 1964, Mergner and Schuhmacher 1974). *In situ* measurements and aerial photography have revealed the existence of areas of vortex formation near islands with fringing reefs as well as zones with strong currents that affect the accumulation of sediments and development of benthic communities (Murray and Roberts 1977, Hamner and Hauri 1981, Roberts et al. 1981). Investigations of the complex reefs of Nicaragua and Barbados Island, conducted by Roberts and co-workers, (Roberts et al. 1975, 1977, Roberts and Suhayda 1977, Suhayda and Roberts 1977) determined the spatial zonation of hydrodynamic processes on a reef slope, the power contribution of different currents and sea states and the degree of dissipation of water motion on different reef sites. Other researchers (Von Arx 1948, Frith 1981, Wolanski 1981) showed the effects of wind drift, roughness, long gravity waves, upwelling and coastal sewage on the structure of currents and thermohaline conditions inside reef lagoons. Some authors (Storr 1964, Mergner and Schuhmacher 1974) stress that wave and current action are the main factors causing biotic zonation of patterns on coral reefs.

Water exchange processes provide reef areas with seawater circulation, thermal exchange and salt transport. The period during which the seawater in atoll lagoons is completely changed may range from several months to several years depending on the lagoon size and circulation speed (Gallagher et al. 1971, Stroup and Mayers 1974, Magnier and Wanthly 1976.) The degree of openness of lagoons produces important hydrological consequences that affect primary productivity. Considerable openness of a lagoon, for example, reduces the range of salinity variations, promotes development of greater biomasses and diversity of phytoplankton which leads to a high concentration of dissolved oxygen (Kwei 1977).

The distribution of major nutrients, such as phosphorus, nitrogen and silicon, are among the factors limiting the primary production of reef systems. For coral islands, the degree of enrichment of waters with nutrients depends on hydrodynamic factors such as: tidal and drift currents, internal inner waves and upwelling (Konnov and Scherbinin 1975, Gusev et al. 1980, Wolanski and Pickard

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1983). Biological nitrogen fixation (Hatcher and Hatcher 1981, Smith 1983), inclusion of organic nitrogen fixation and phosphorus into the production cycle through bacterioplankton, periphyton and filter-feeding animals (Sorokin 1977, 1986, Atkinson 1981) are intrinsic sources of nutrients. Partially closed cycles of nutrients within symbiotic animals such as molluscs and corals (Sorokin 1986) that dominate benthic production, result in nutrient ratios that differ from Redfield's ratio of C:N:P = 550:30:1. This enables the fixation of more organic carbon per unit of biomass than in planktonic systems (Smith 1983), even in waters depauperate in nitrogen and phosphorous.

STUDY AREA

During the northeastern monsoon conditions (November-March), the Seychelles Plateau is under the influence of the inter-tradewind equatorial counter-current which runs eastward. According to the data of different authors, the south boundary of this current in December-January is variable and ranges between about 8-10°S (Burkov 1982, Marsac et al. 1983, Potier and Marsac 1984). To the south, there is a south trade-wind current which crosses the Indian Ocean in a westerly direction. During winter, the axis of this current, where speeds are highest, lies at approximately 10°S (Burkov and Neyman 1977). A tropical front is situated between these opposing currents (7-12°S). This zone separates surface waters of low salinity, but high oxygen levels, of the northern Indian Ocean (Burkov 1982). The frontal boundary changes its position depending on climatic conditions during different years. The result is an increase in complexity of interannual and intraannual current patterns and areas of divergence and convergence that result in the upwelling of deep waters and the thickening of surface water layers, respectively, near the Seychelles Islands.

Vertical temperature structure of waters over shallow bottom sites consists of two layers. The surface layer is homogeneously warmed up to 27-30°C and its thickness is usually 30-40 m but may be as shallow as 20 m (Marsac and Hallier 1985). Deeper subsurface south subtropical intermediate water has a temperature of 12-14°C and a temperature gradient of 2.2 to 2.4°C per 10 m (Marsac and Hallier 1985). The investigations carried out in January near the equator revealed the existence of temperature fluctuations with a 2 h period and vertical amplitude of oscillation up to 40 m which become greater in the regions of intensive currents and at the upper boundaries of seasonal thermoclines (depth 105-115 m). Short-term fluctuations of temperature with a wave-like nature (amplitude of up to 7 m, Morozov et al. 1977) also were found.

Under southeastern monsoon conditions, equatorial counter-current waters have high salinities, while the south tradewind current shows lower salinities (Burkov and Neyman 1977). Subsurface south subtropical intermediate waters have high salinities since they are formed in a subtropical zone where evaporation exceeds precipitation. Additionally, transformed high salinity water of the subsurface Arabian intermediate water mass (more than 36.5 ppt.), is found (Burkov 1982) near 10°S latitude and running along the equator from the west. During the expedition, three morphological types of island system were investigated: (a) granitic islands with fringing reefs (Mahé, Praslin, La Digue); (b) sandy islands with platform reefs (Providence, African Banks, Desroches, Coëtivy) and (c) atolls (Farquhar, St. Joseph, Aldabra, Astove, Cosmoledo).

METHODS AND MATERIALS

Currents

Currents were recorded by recording current meters, both in the water column and in the bottom layer 0.5 m above the bottom. The interval of measurements was 15 min, and the duration of a recording ranged from 17 h to 8.5 days. Table 1 summarizes the descriptive characteristics of the sta-

tions. In addition to the hydrological investigations, hourly observations of wave and wind conditions were recorded for 24 h periods.

To estimate the structure, direction and speed of currents, a distribution density of direction probability function ($P=y$) and of modulus of current speed ($P=v$) (Bishev et al. 1977) were used. Turbulent features of water currents were estimated using a number of indices calculated for meridional (u) and zonal (v) components of a current velocity vector, including turbulence intensity, coefficients of horizontal turbulent exchange and coefficients of horizontal turbulent exchanges per hour. Intensity of turbulence ($J_{u,v}$) is a ratio of the quadratic mean deviations of rate pulsations to the average current rate. According to the tensor theory of turbulence, coefficients of horizontal turbulent exchange calculated by the method of Ertel-Shtokman (Ertel 1932, Shtokman 1940) represent the process of exchange of motion quality as an ellipse. The major axis corresponds to A_{\min} , the minor axis to A_{\max} . The ratio A_{\max}/A_{\min} determines the degree of anisotropy of horizontal turbulent exchange (ϵ).

To reveal the effect of different scale vortices on the processes of horizontal turbulent exchange, the series of rate components were averaged before treatment using a cosine filter periods of averaging (T_o) of 2, 6, 12, 24, 48 and 96 h (Ozmidov 1968). The structure of water flow and contribution of different scale vortices to turbulent energy were estimated using calculations (S_w). Reliability of the function maxima was determined at the 95% confidence interval.

Thermohaline structure, salinity and hydrochemical characteristics

Temperature, salinity and hydrochemical characteristics of waters were recorded at 24 coastal hydrological stations and on transects across major geomorphological zones of reef shallows. Separate hydrological sampling was conducted down to 200 m beyond the intertidal zone to record temperature, salinity, pH and dissolved oxygen. A water quality monitor and bathythermographs Tsurumi Seki, (model 2) were used in addition to a portable TS-probe and portable thermometer Watanabe Keiki Mgf.

Water samples for determinations of nutrient concentration were collected using bathometers, a submersible pump and SCUBA divers. Concentrations of phosphorus (general, inorganic and organic), nitrogen (ammonium, nitrite, nitrate and organic) and dissolved silicon were analyzed. The interval between sampling was 3 h, and samples for nutrient determination were taken every 6 h according to the phases of a given tidal cycle.

Samples were analyzed using the modifications of methods adopted in Strickland and Parsons (1972). Ammonium, phosphorus and nitrites were determined spectrophotometrically, nitrates were reduced to nitrites in a capillary column containing copper wire covered with cadmium layer (Anon. 1979). Silicon was determined by the improved method using ascorbic acid as a reducer, whereas organic nitrogen and phosphorus were analyzed according to the methods of Walderrama (1981).

A photometer with a silicon photodiode was used to estimate the vertical distribution of light in the water column. Spectral characteristics of sensitivity were determined by a filter having maximum penetration in the range of 550 nm. Measuring illumination in water, we at the same time controlled outward illumination. Obtained data were used to calculate light indices (K) according to Jerlov (1980).

RESULTS AND DISCUSSION

Fringing reefs of granitic islands (Mahé, Praslin and La Digue Islands).

Coastal reefs redistribute wave energy and redirect currents from the open sea into shallow waters. Water exchange is most intensive at the outer edge of a reef crest in the area of strong wave and current influence.

Station 10, near the south coast of Praslin Island, is subjected to the effects of a strong southeasterly current with periodic tidal reversals (Table 2). Mean current speeds are $17-21 \text{ cm}\cdot\text{sec}^{-1}$, maximal speeds reach $28-32 \text{ cm}\cdot\text{sec}^{-1}$. This current shows a high degree of stability ($J_{v,u} = 0.36-0.50$) under horizontal turbulent exchange ($A_{\max} = 10^4-10^6 \text{ cm}^2\cdot\text{sec}^{-1}$).

At sites protected from wave action, movement of water near the bottom becomes progressively weaker. At the western point of St. Anse Bay, *Sargassum* communities were exposed to weak unstable flows ($J_{v,u} = 8.5-9.4$) and typical current speeds over the bottom did not exceed $2-4 \text{ cm}\cdot\text{sec}^{-1}$. Horizontal turbulence also was weak at this site, on the average about 42 times weaker than in the open subtidal zone (Table 2).

Stronger coastal currents are typical of shallow bottom sites between islands. For example, the northeasterly flow between Cerf and St. Anne Islands ranged between 15 and $22 \text{ cm}\cdot\text{sec}^{-1}$. (Fig. 1, Table 2). On the average, turbulent flow during the northwesterly flow was higher ($A_{\max} = 2\cdot 10^5 \text{ cm}^2\cdot\text{sec}^{-1}$; $J_{v,u} = 1.13-1.35$) than that of the northeasterly one ($A_{\max} = 1.6\cdot 10^5 \text{ cm}^2\cdot\text{sec}^{-1}$; $J_{v,u} = 0.42-0.50$).

Turbulent processes over fringing reef platforms depend on energy mainly from tidal, drift and wave currents (Fig. 2). At most of the open sites (e.g., Praslin Island, St. 10) some influx of turbulent energy was documented even over averaging periods of more than 12 h, probably dependent on the effects of large scale oceanic circulation. The structure of pulsations in current speeds depends on tidal processes with typical periods of 12 and 6 h, wind drift effects with a period of about 24 h and other weather-related variations with 40-45 h periods (Fig. 3). High-frequency current fluctuations are probably due to orographical vortex formation and wave currents with 1-3 h periods.

Horizontal turbulent exchange in the areas studied is anisotropic due to its intensity (Table 2). The direction of maximal exchange approaches that of a dominating flow. For the same reason, the vortex structure of water motion near Mahé and Praslin is most clearly displayed as a spectrum of zonal components of current speeds, thermohaline conditions, hydrochemical features and optical characteristics.

Thermohaline conditions, hydrochemical and optical characteristics.

The surface equatorial waters near the south coast of Praslin Island showed daily temperatures ranging from 28.3 to 29.7°C and daily salinities from 35.05 to 35.17 ppt. During the absence of intensive wind mixing, temperature and salinity characteristics depend on insolation. The maximum temperature (29.7°C) in the surface layers was observed at 1700 hrs local time, the minimum (28.6°C) occurred at 1500-1800 hrs. During the daytime, intensive evaporation from the surface caused formation of a more saline layer (up to 35.2 -ppt) which sank to lower levels and became cooler at night. Tidal mixing equalized thermohaline parameters throughout the water column.

Values of pH ranged between 8.3 and 8.4 . Dissolved oxygen concentrations varied from 101 to 108% of saturation (Fig. 4C). The maximum near the bottom (107%) was observed in the afternoon

and the minimum (101%) occurred during night and early morning hours, consistent with daily fluctuations of photosynthetic activity. Oxygen concentrations in the surface waters ranged from 104 to 108% during 24 h, with maxima at 400 hrs and minima at 1000 hrs.

Near La Digue Island, the salinity was somewhat higher (35.23 - 35.31 ppt) and off the south coast temperatures of the surface waters and near the bottom did not vary greatly between 1400-1600 hrs local zone time (28.1°C at 15-30 m to 28.4°C at the surface). The dissolved oxygen concentration was similar in absolute values (4.52-5.06 mg·l⁻¹) to that observed near Praslin Island (102.2-112.2% of saturation), whereas pH values ranged between 8.32 and 8.38.

A change in the optical type of the waters near Praslin Island occurred at 3 m in depth, with the surface layers corresponding to the type III coastal waters (K=0.200). Water layers deeper than 3 m corresponded to the type II oceanic waters (K=0.094).

Nutrient concentrations near Mahé, Praslin and La Digue Islands ranged within the following limits: phosphates in the surface waters ranged from 0.07 to 0.35 $\mu\text{g atom}\cdot\text{l}^{-1}$; organic phosphorus - 0.04 to 0.22; silicon 1.6 - 3.0; nitrites 0 - 2.0; nitrates 0 - 0.55; ammonia 0 - 3.0; and organic nitrogen 5.4 - 23.0. Near Praslin Island, under conditions of good water exchange, concentrations of phosphorus and silicon were constant throughout the water column down to 23-25 m. Waters near Victoria Harbor (Mahé Island) were the richest in nutrients and contained the highest phosphate and silicon concentrations (Table 3). Lower phosphate and nitrogen concentrations were recorded in the waters of Praslin and La Digue Island. Nitrites were not found near these islands, and nitrates and ammonia were observed only in the surface waters or at intertidal sites where seagrasses and algae grew. At low tide, regenerative capacity in the bottom sediments was indicated by considerable amounts of ammonia (up to 3 $\mu\text{g atom}\cdot\text{l}^{-1}$ - in bottom Cœtivy layers) where the concentration of organic nitrogen dropped from 15 to 8 $\mu\text{g atom}\cdot\text{l}^{-1}$. An increase in concentration of all nitrogen forms was observed southwards from Victoria Harbor (Mahé Island): nitrites from 0.10 to 0.13 $\mu\text{g atom}\cdot\text{l}^{-1}$; nitrates 0.36 - 0.55; and organic nitrogen 14.4 - 23.0. On the whole, the richest nutrient waters were observed in the most developed portions of the eastern and southeastern coasts of Mahé subjected to the effects of coastal sewage. The least nutrient concentrations were found in the waters of La Digue Island which is situated at the edge of a granitic fragment where there is a good exchange with oligotrophic oceanic waters.

Reefs of sandy islands (Cœtivy, African Banks, Providence, Desroches)

Cœtivy, Providence and African Banks have similar bottom topographies. They arise as wave swept sandy bedforms on shallow platforms of coral origin which form on top of underwater mountain ranges. Their coasts are fringed with coral-dominated reefs in different developmental stages and their platforms are covered with patches of coral communities and macrophytes. The nearshore circulation surrounding these islands have high hydrodynamic activity. During the present study, the east coast of Cœtivy Island was subjected to a strong northeastern current (Fig. 5, St. 2). Mean flow speeds in the upper 10 m layer of water were 34-42 cm·sec⁻¹ and deeper (30 m) they reached 44-63 cm·sec⁻¹ with maximal pulses 1 m·sec⁻¹ or more. Southeast of the South Island of African Banks at the seaward edge of a vast underwater terrace (St. 14) a strong eastward current with a mean speed of about 30 cm·sec⁻¹ was recorded. High current energy at the edges of island platforms results in the development of considerable turbulence. Thus, the coefficients of horizontal turbulent exchange near Cœtivy Island and African Banks ranged from 10⁴ to 10⁶ cm²·sec⁻¹. It is interesting that near Cœtivy Island, turbulent processes reach maximal activity in the middle water layers. Exchange coefficients at a depth of 30 m are 3 times greater than at 10 m in depth. The pulse-rate intensity at the edge of a coral plateau (African Banks, $J_{v,u} = 0.82-1.20$) and in the subsurface layer over a reef slope (Cœtivy, $J_{v,u} = 0.97 - 1.06$) exceeds values at the water surface

(Cöetivy, $J_{v,u} = 0.47-0.57$).

Water motion over island platforms showed less activity. Thus, the windward western coast of Cöetivy Island is bathed by a north/northeasterly current (Fig. 5, St. 1), with mean speeds of $10-25 \text{ cm}\cdot\text{sec}^{-1}$ and maximal values ($32-38 \text{ cm}\cdot\text{sec}^{-1}$) observed both at the surface and at the lower layer of the current. In the bottom layer, the current changes direction to southeast and its speed does not exceed $4 \text{ cm}\cdot\text{sec}^{-1}$.

Tidal variability of currents (Fig. 5, St. 3) increases at coastal promontories of the island where currents can change direction from northwest to southeast at mean speeds of $20-26 \text{ cm}\cdot\text{sec}^{-1}$. Horizontal turbulent exchange in the surface layer (10 m) over the western reef flat of Cöetivy Island is almost 3 times less than for the same depth in waters of the eastern coast. In the middle layers this difference increases and becomes 6-fold greater (Table 2). Exchange coefficients range from 10^3 to $10^6 \text{ cm}^2\cdot\text{sec}^{-1}$, but immediately over the bottom of the reef platform they decrease to $10^2-10^3 \text{ cm}^2\cdot\text{sec}^{-1}$, with the current becoming more unstable ($J_{v,u} = 1.23 - 1.39$). Near the bottom, turbulent processes within the zone of coastal coral communities (5-8 m) exceed turbulent levels at the boundary of coral distribution, on average, by 300 times and show maximal variability because of bottom roughness.

In cases where island plateaus on relic lagoon bases, as happens near the northwestern coast of Desroches Island, circulation around the island shows slower current speeds. Near the northwestern coast of the island, water motion reverses with the current direction changing from southwestern to north-eastern at mean speeds of $2-5 \text{ cm}\cdot\text{sec}^{-1}$ and maximal ones at $22-25 \text{ cm}\cdot\text{sec}^{-1}$ (Table 2, St. 7). Near the bottom, the current turns toward the east and southeast and becomes more stable with mean speeds of to $6-14 \text{ cm}\cdot\text{sec}^{-1}$. Periodic wave currents with high speeds appear on coastal shallows with gentle bottom slopes during storm conditions as, for example, the current of up to $50 \text{ cm}\cdot\text{sec}^{-1}$ that was recorded over a *Thalassia* meadow near the northwestern coast of Desroches Island at a depth of 4.5 m during a period of northwesterly winds (Table 1, St. 8). Also a very weak current ($2-4 \text{ cm}\cdot\text{sec}^{-1}$) running northeastward (Table 2, St. 9) is present near the opposite leeward (southeastern) coast, separated by a reef crest. Currents over the sunken lagoon have high pulse capacities ($J_{v,u} = 6.27$ to 6.57) demonstrated by a variable range of coefficients of turbulent exchange ($10^4-10^5 \text{ cm}^2\cdot\text{sec}^{-1}$). Near the bottom, turbulent exchange decreases ($A_{\max} = 10^3-10^4 \text{ cm}^2\cdot\text{sec}^{-1}$), whereas maximal coefficients of turbulent exchange were observed near the northwest coast of the island, in the zone of wave-induced currents ($A_{\max} = 10^5-10^6 \text{ cm}^2\cdot\text{sec}^{-1}$). Near the leeward southeastern coast, turbulence was weak with the orientation of maximal turbulent exchange being both longitudinal and nearly diametrically opposed to the direction of the dominating current. The degree of anisotropy of turbulent exchange increases with decreasing distance to the coast.

Turbulent vortices in the coastal zones of calcareous islands are caused mainly by tidal processes with periods of 12-24 h (Fig. 6). The effect of hydrodynamic processes on a large synoptical scale (average recording period of 48 h or more) is not as pronounced. Tidal cycles (with fluctuation periods of 3.5-4, 12 and 16 h) play the most important role in the structure of turbulent fluctuations observed in a given current. Additionally, functions of spectral density of speed pulsation reveal the presence of large vortices with periods of 16-18, 27-28 and 30-35 h as well as orographic and wave pulsations of a given current (periods of 1-3 h).

Thermohaline conditions, hydrochemical and optical features.

Analysis of data from the reef flat on the western coast of Cöetivy Island showed an absence of significant temperature stratification. Wind and wave action caused mixing of warm and less saline surface waters (temperature greater than 27.5°C , salinity less than 34.9 ppt) down to 15-25 m in

depth (Fig. 8 A, B, St. 1). Deeper, there were colder ($25-26^{\circ}\text{C}$) and more saline (greater than 34.95 ppt) waters. Near the western coast of the island, surface water temperatures increased from 27.54 to 28.10°C . Some decrease in salinity was observed due to precipitation. Vertical temperature variability was influenced little by tidal processes.

The eastern slope of Cœtivy Island was much more affected by hydrological processes of the open sea. For example, on 16 January 1989, at the reef crest, an intensive input of cooler and more saline waters characteristic of the south subtropical intermediate water mass was observed (minimal temperature 15.4°C , salinity 35.21 ppt), which probably was caused by upwelling of deep waters due to strong (up to $25\text{ m}\cdot\text{sec}^{-1}$) westerly winds and tidal processes (Fig. 9 A, B, St. 2). The same phenomena resulted in a 4.19°C temperature difference between the surface and a depth of 10 m at a station 300 m off the leeward eastern coast. The temperature gradient between surface and deep waters was $2-2.5^{\circ}\text{C}$ per 10 m. On the whole, waters of the eastern coast were cooler and more saline than those of the western coast.

Oxygen concentrations near the eastern coast of Cœtivy Island conform well to the temperature patterns described above. During the entire period of study, the oxygen concentrations at the surface exceeded 100% saturation. The minimal value (60.5%) correlated with an influx of cooler waters found at a depth of 44 m (Fig. 9 C). Near the western coast of Cœtivy (Fig. 8 C, St. 1) an oxygen deficiency was observed which shifted towards the surface layers during the night (up to 92.3% saturation at 1.3 m in depth). The minimal oxygen concentration (77%) was found near the bottom (30 m) at 300 hrs local time on 13 January 1989.

Values of pH near Cœtivy Island were 8.27-8.32 but towards the coast they decreased to 8.06. However, in warm intertidal pools, rich in all nitrogen forms as well as phosphates, pH reached values of 8.75-9.02.

Penetration of cool subsurface waters into shallow areas was recorded near Cerf Island (Providence, 19.6 m depth), as well as near Cœtivy Island. The difference between near-surface (28.45°C) and near-bottom temperatures was 4.4°C . The presence of upwelling of transformed deep waters is also confirmed by a sharp drop (to 87.5% saturation) of oxygen concentration in near-bottom waters. Salinities seaward of Cerf Island ranged from 34.76-34.83 ppt. At the surface near the coast, salinity varied from 34.6 to 34.7 ppt, temperature - from 28.3 to 29.8°C and near the bottom from 34.5 to 34.7 ppt and from 27.9 to 28.1°C . pH varied slightly (from 8.2 to 8.28).

The coastal area of South Island (African Banks) was homogeneous in thermohaline features up to the boundary of the reef plateau (16 m depth). During a 24 h survey, seawater temperatures ranged between $27.9-28.1^{\circ}\text{C}$ and salinity varied between 35.12 to 35.48 ppt. Oxygen concentrations were 100-107% saturated and the pH varied from 8.22 to 8.29.

Transformed equatorial subsurface waters found along the northwestern shallows of Desroches Island showed highly homogeneous temperatures ($27.4-28.9^{\circ}\text{C}$) and salinities (34.88-34.99 ppt). Variability of thermohaline indices was slight in seaward and coastal areas, which suggest an efficient water exchange. The amplitude of the 24 h temperature range near the water surface was 1.5°C (from 28.6 to 30.1°C), near the bottom - 0.5°C (from 27.6 to 28.2°C), while the salinity deviated only 0.07 ppt over the entire water column and the pH ranged from 8.3 to 8.4.

Near Cœtivy Island, the optical boundary of the change in water type is at approximately 6 m in depth. In the upper layers, K is 0.115, which corresponds to coastal type I water. Deeper than 6 m, there is a layer corresponding to ocean type I water ($K=0.057$). Near Providence, the optical types of water masses were similar to those of Cœtivy: the surface water layer (6 m deep) corresponded to coastal type I water ($K=0.135$) and deeper there were clearer waters of the ocean type I ($K=$

0.047). Off the coast of African Banks, the optical type changed at a depth of than 1.8 m with waters of coastal type III ($K = 0.168$) below and waters of coastal type IX ($K = 0.791$). Around Desroches Island, the optical type of waters changed at the 3 m depth where the less saline and more turbid upper surface layer corresponded to the coastal type V ($K = 0.250$) and waters of ocean type III were observed deeper than 3 m.

This study did not reveal consistent differences in concentrations of nutrients for islands of different origin, i.e., coral vs. granitic (Table 3), since both types had habitats of both low and high enrichment (e.g., upwelling, birds, sewage). The greatest range of diurnal and spatial variability of nutrients was found near Cœtivy Island where waters were rich in phosphates and silic acid, 0.4 and $3.74 \mu\text{g-atom}\cdot\text{l}^{-1}$, respectively. The highest concentrations were observed in intertidal and upper subtidal zones and especially in warmed intertidal pools where high concentrations of all forms of nutrients (phosphorus, nitrogen, silicon) were found. The pH values reached 9.0 which suggests high levels of production processes. The greatest biomass of macrobenthos (especially of *Thalassodendron ciliatum*, reported by Gutnik et al., Ch. 5 this issue) was also found in the intertidal zone of Cœtivy.

The source of phosphates in the coastal waters of Cœtivy Island is partly to an influx of deep waters rich in nutrients, which was observed both at the eastern dropoff or along the shallow western coasts (Table 4).

The coastal waters of Cerf Island (Providence Group) are notable for their high levels of nitrates and organic nitrogen: 0.59-0.88 and $16.8\text{-}17.5 \mu\text{g-atom}\cdot\text{l}^{-1}$, respectively (Table 3). Higher concentrations of phosphates and nitrates in surface waters were observed near the reef crest on the southeastern side of the island, and reached 0.25-0.27 and $0.83\text{-}1.16 \mu\text{g-atom}\cdot\text{l}^{-1}$, respectively. Additionally, in shallow waters 300-500 m offshore, at a depth of 0.7-2.5 m, the phosphate concentration also increased.

The coastal surface waters of South Island (African Banks) have low mean levels of phosphates and silicon: 0.14 and $1.37 \mu\text{g atom}\cdot\text{l}^{-1}$, respectively (Table 3). In shallow waters, higher concentrations of organic phosphorus were found, and highest levels for African Banks occurred in immediate proximity to the coast: 0.29-0.21 $\mu\text{g atom}\cdot\text{l}^{-1}$. Concentrations of silicon, ammonia, nitrates and organic nitrogen did not change as a function of the distance from the shore and nitrites were absent.

According to the 24 h survey southeast of African Banks, the concentrations of phosphates, silicon and nitrates in the surface waters and near the bottom did not change substantially throughout the day and ranged from 0.08-0.18, 1.2-2.55 and $0.02\text{-}0.08 \mu\text{g-atom}\cdot\text{l}^{-1}$, respectively. An inverse relationship was observed in the 24 h variation of organic phosphorus and nitrogen concentrations.

The concentrations of nutrients in the coastal waters of Desroches, both on the windward and leeward sides, were similar in mean values to those for the other islands studied. The 24 h variation of nutrients in the lagoon area at 0, 10 and 25 m depths showed maximal variability at the 10 m depth. At this level, 24 h variations of inorganic and organic phosphorus ranged from 0.16 to 0.54 and 0.02 to $0.39 \mu\text{g-atom}\cdot\text{l}^{-1}$, respectively, changing in inverse relation but without apparent regularity. Phosphorus and silicon concentrations in both surface and bottom waters were stable and did not change over time. The 24 h observations of nutrients were carried out at windward and leeward island sites 150-200 m offshore. Silicic acid concentrations in coastal waters varied from 2.05 to $4.45 \mu\text{g-atom}\cdot\text{l}^{-1}$. Phosphorus values (both organic and inorganic) were similar at both stations and corresponded to the photosynthetic pattern, with minimal PO_4 -levels recorded at 2000 hrs, at the highest oxygen concentration. During the night, phosphate concentrations increased,

probably due to the destruction of organic phosphorus, which was in inverse concentration to that of phosphates. The fluctuation of PO_4 -concentrations was somewhat greater ($0.11\text{--}0.61\ \mu\text{g-atom}\cdot\text{l}^{-1}$) while that of nitrates was smaller ($0\text{--}0.77\ \mu\text{g-atom}\cdot\text{l}^{-1}$) on the leeward side than on the windward side. These differences are likely to be the result of higher current speeds on the windward side and more active mixing and water exchange between the submerged lagoon and open ocean waters. In contrast, to the less dynamic coastal waters of the southeastern side are protected by the island and reef from wind and wave action.

Atolls (Farquhar, St. Joseph, Cosmoledo, Aldabra and Astove)

Atoll islands are widely distributed in the Indian Ocean. Farquhar, St. Joseph, Cosmoledo, Astove and Aldabra have shallow lagoons connected with the open ocean by one or several channels. Oceanic process affect only the outer slopes of the atolls whereas hydrological conditions in the lagoons separated from the ocean by land or by the reef platform mainly depend on tides cycles, winds, evaporation and precipitation.

The outer reef slope of the eastern coast of Farquhar Atoll is washed by a strong ($50\text{--}70\ \text{cm}\cdot\text{sec}^{-1}$) northeasterly current. Mean current speeds of St. Joseph's southeastern coast range between $24\text{--}36\ \text{cm}\cdot\text{sec}^{-1}$ (Fig. 10, St. 15). Near Wizard Island (Cosmoledo Atoll), the southwesterly current speed was $17\text{--}31\ \text{cm}\cdot\text{sec}^{-1}$ (Fig. 11, St. 18). Typical current speeds near the eastern coast of Aldabra Atoll were $15\text{--}30\ \text{cm}\cdot\text{sec}^{-1}$. Localized turbulent vortices and tidal fluctuations caused short term increases in current speeds of $1\ \text{m}\cdot\text{sec}^{-1}$ or more in all areas under study.

Near the bottom, current speeds decreased considerably. For example, rough coral substrata near Farquhar Atoll at 18 m in depth reduced the current speed to $2\text{--}4\ \text{cm}\cdot\text{sec}^{-1}$ (St. 6). In the narrow channel between D'Arros Island and the western coast of St. Joseph Island, the speed of a reverse current near the base of a coastal coral-dominated reef ranged between 2 and $9\ \text{cm}\cdot\text{sec}^{-1}$ (Fig. 10, St. 16). The reef crest is characterized by increased hydrodynamic activity. On the southeast coast of Cosmoledo Atoll, the reef is characterized by higher water exchange due to an offshore current coming onto the reef platform and dividing into many differently directed flows with speeds of around $25\text{--}35\ \text{cm}\cdot\text{sec}^{-1}$. Closer to the coast, the dissipation of water motion energy continues. Maximal current speeds in the study areas of Farquhar and St. Joseph reef-flats did not exceed $14\ \text{cm}\cdot\text{sec}^{-1}$ (St. 5 and 17).

Coefficients of horizontal turbulent exchange over outer atolls slopes were in the order of 10^4 to $10^7\ \text{cm}^2\cdot\text{sec}$, decreasing with an increase in protection from wave action (Farquhar - 1.1×10^6 , Cosmoledo - 1.3×10^5 , St. Joseph - 8.9×10^4 , Aldabra - $3.8 \times 10^4\ \text{cm}^2\cdot\text{sec}^{-1}$). Pulsation patterns of currents depend on their inherent stability. On outer atoll reef slopes in deep water with stable currents, the turbulence is usually less than on shallow reef platforms.

The greatest current speeds in atoll lagoons can be observed in direct proximity to channels which provide lagoons with water influx and outflux during each tidal cycle. Observations made in the large lagoon of Cosmoledo Atoll revealed the presence of strong tidal currents with mean speeds of $2\text{--}15\ \text{cm}\cdot\text{sec}^{-1}$ (strongest currents of $24\text{--}27\ \text{cm}\cdot\text{sec}^{-1}$) which provide active mixing ($A_{\text{max}} = 1.7 \times 10^4\ \text{cm}^2\cdot\text{sec}^{-1}$). At the same time, in some lagoon sites separated by temporary barriers and shallows, water currents tend to be weak. This phenomenon promotes the accumulation of fine-grained sediments. One such example is the western side of St. Joseph Atoll, where current speeds did not exceed $2\text{--}4\ \text{cm}\cdot\text{sec}^{-1}$ and the average value of coefficients of horizontal turbulent exchange was $8 \times 10^2\ \text{cm}^2\cdot\text{sec}^{-1}$ (Fig. 10, St. 17). The influx of turbulent kinetic energy ceases for values of averaging periods from 2 to 24 h (Fig. 12), suggesting that the main processes causing instability of the water column near atoll coasts are tides, winds and wave currents. Anisotropy of turbulent exchange is

most distinctly displayed in areas of stable current action. The direction of maximal turbulent exchange to a large degree coincides with the current direction in cases of strong current.

Distribution functions in the spectral density of kinetic energy due to turbulent pulsations in current speeds reveal a 12 h period as a main peak of energy supply (Fig. 13). Farther offshore, additional sources of large scale current pulsations are vortices with 14-18 h periods (resonance or orographic). Tidal modes of smaller periods (6-7 or 3-4 h) and currents of wind-wave origin (1-2 h) can be found at shallow depths. Inside the lagoon of St. Joseph Atoll, the main effect on hydrodynamics is probably produced by wind action with a period of 24-25 h, and in the lagoon at Cosmoledo 30-35 h fluctuations related to weather conditions were observed.

Thermohaline conditions, optical and hydrochemical features.

Lagoons produce a substantial effect on the physical-chemical characteristics of coastal waters of atolls. Lagoons are regions in which waters coming in from the open ocean become transformed, depending on the degree of isolation and meteorological conditions. Thus, in the rainy period of 22 January 1989, at the northeastern part of Farquhar Atoll's lagoon, the salinity did not exceed 33.85 ppt at a depth of 0.8 m, and during the stable sunny weather of 12 March 1989, salinity reached 36.3 ppt at the surface in the central part of the lagoon, while near the bottom (5 m depth) it was 38.66 ppt. On the whole, the temperature and salinity of surface waters ranged from 26.2-27.6°C and 34.77-35.04 ppt, respectively.

At low tide, lagoon waters penetrate into the outer boundary waters of atolls and alter their thermohaline structure. Thus, active turbulence near atoll coasts causes mixing of warm lagoon waters to greater depths levels and the appearance of temperature inversions (Fig. 14, St. 4), e.g., at 10 m in depth the temperature was 27.3°C while at 30 m in depth it was 27.6°C. Near the bottom (45-50 m), an influx of cool (23-24°C) surface south subtropical waters was observed. Stronger winds causes an increase of the temperature gradient ($1.4^{\circ}\text{C}\cdot\text{m}^{-1}$) in the contact zone between different water masses.

During the daytime, a reduced level of dissolved oxygen was observed around Farquhar at 15-25 m in depth. In the second half of the day, the boundary of 100% oxygen saturation was lowered to the 50 m level. Maximal oxygen concentrations coincided with the period of maximal intensity of photosynthesis, while pH values ranged between 8.42-9.38.

Near Astove, thermohaline characteristics changed from the channel to the lagoon. In the shallow lagoon at 1 m in depth, the salinity was 35.1 ppt and temperature 32.3°C; in the surface layer of the lagoon area of the channel, salinity was 35.5° ppt and temperature was 35.2°C; in the seaward part of the channel - 35.2 ppt and 31.4°C; and at 2.5 km westwards from the channel - 34.7 ppt and 29.2°C. The high photosynthetic intensity during the daytime caused a considerable oxygen oversaturation of lagoon waters of up to 132%.

Active water mixing near Cosmoledo Atoll resulted in lagoon temperature fluctuations from 29.1 to 30.6°C, and salinity changes from 34.5 to 34.8 ppt while in outer coastal zone, temperatures ranged from 29.0 to 29.2°C and the salinity was 34.9 ppt. Oxygen saturation levels of waters at Station 18 (Cosmoledo Atoll) ranged from 101-103% saturation down to a depth of 20 m. The pH ranged between 8.3-8.4. Similar to findings near Cosmoledo, a high degree of homogeneity (salinity= 35 ppt) was observed in the surface lagoon waters and outer reef slope waters of St. Joseph Atoll. The range of temperature fluctuations at the surface was 0.4°C (from 27.8 to 28.2°C) and near the bottom 0.3°C (from 27.6 to 27.9°C). Salinity at the surface ranged from 35.24 to 35.46 ppt, near the bottom it was 35.45 ppt. Oxygen saturation levels of surface waters were 104-106% and

100-102% near bottom. The pH varied between 8.2 and 8.4.

The most characteristic features of vertical thermohaline structure of waters near South Island (Aldabra Atoll) were cyclic temperature and salinity patterns in near bottom waters with a fluctuation period of about 12 h and amplitude of 4°C (23.5-27.5°C). The upwelling of cooled subsurface waters corresponded to low tide waters and downwelling occurred during high water. Fluctuations became appreciable below 20 m in depth. Shallower there was a homogeneous temperature layer (27.7-27.9°C) with a salinity of 34.94 to 34.99 ppt. The influx of cooled waters was caused by upwelling from the upper zone of intermediate south subtropical waters. Their deepwater origin is indicated by both a salinity increase (up to 35.08 ppt) with a sharp drop in oxygen concentration (down to 85% saturation) in the bottom layer, while oxygen saturation at the surface was 108-110%.

The optical characteristics of the various atolls studied displayed vertical differences. For example, the subsurface waters of Farquhar Atoll related to the ocean type II ($K = 0.098$) down to 6 m in depth, near Aldabra Atoll, the surface layer to 3 m was occupied by waters of coastal type VII ($K = 0.462$), and at Cosmoledo Atoll surface waters were coastal type I ($K = 0.138$) down to 8.2 m in depth. In these regions, bottom waters were ocean type I ($K = 0.047$ - 0.052). St. Joseph and Astove Atolls were similar to ocean optical type III subsurface waters ($K = 0.101$ - 0.106). The 7 m surface near Astove corresponded to the coastal type III ($K = 0.189$) and at St. Joseph the surface layer was the coastal type V ($K = 0.256$) to 1 m in depth.

The lagoon waters of these atolls, as a rule, had unique hydrochemical features in comparison with waters surrounding their atolls as well as between each other in terms of chemical composition and productivity. High concentrations of inorganic phosphorus, silicon and organic nitrogen were observed in Farquhar Lagoon, where the highest productivity of phytoplankton occurred (communication of V. M. Gol'd), an influx of deep oceanic waters enriched with phosphates was observed here during maximal low waters near the southeastern coast of the atoll at 50 m in depth (Table 5).

High concentrations of organic phosphorus were found in the coastal and lagoon waters of Cosmoledo Atoll (0.74 - $0.85 \mu\text{g-atom}\cdot\text{l}^{-1}$) and Astove Atoll (0.29 - $0.73 \mu\text{g-atom}\cdot\text{l}^{-1}$), which are obviously related to the great number of nesting colonies of birds at these islands. Astove Atoll has a submerged shore line with a steep slope which provides quick dispersion of organic phosphorus in deep waters and, as a result, a considerable difference between concentrations of organic phosphorus in the lagoon versus the surrounding waters. Organic nitrogen concentrations were also high but varied considerably (8 - $17 \mu\text{g-atom}\cdot\text{l}^{-1}$). High concentrations of nitrates (0.5 - $0.9 \mu\text{g-atom}\cdot\text{l}^{-1}$) and ammonia were found only in the surface layers (Cosmoledo - 0.36 - $0.90 \mu\text{g-atom}\cdot\text{l}^{-1}$; Astove - 0.94 - $1.63 \mu\text{g-atom}\cdot\text{l}^{-1}$) and suggest a high rate of transformation of organic nitrogen of birds excreta into other nitrogen forms. Similarly, high levels of nitrates ($1 \mu\text{g-atom}\cdot\text{l}^{-1}$) and organic nitrogen (15 - $17 \mu\text{g-atom}\cdot\text{l}^{-1}$) in the coastal and lagoon waters of Aldabra, without a simultaneous increase in phosphorus concentrations, may be the result of activities of nitrogen-fixing microorganisms.

It is known that tidal exchanges can lead to nutrient enrichment of lagoon waters from oceanic sources, filling the lagoon during high tide and creating conditions for increases in primary productivity. During low tide, waters depauperate in inorganic elements leave the lagoon. Silicon concentrations in Aldabra Lagoon followed this pattern; during high tide silicon increased from 1.75 to 2.1 - $2.5 \mu\text{g-atom}\cdot\text{l}^{-1}$ and dropped at low tide. This relationship was not found for other nutrients (Table 6).

At the same time, 24 h observations in the channel to Farquhar Lagoon showed that during low tide the outer side of the atoll was enriched with nutrients running out of the lagoon, whereas during

high tide, oceanic surface waters poor in nutrients entered the lagoon (Table 7).

It is obvious that oligotrophic oceanic water masses surrounding tropical reefs ultimately eliminate differences in nutrient supply between islands of different origins i.e., calcareous or granitic. Lagoon waters retain an individuality which depends both on the exchange processes with the ocean expressed during tidal cycles and on complex biotic conditions in the lagoons and on atoll coasts. Intertidal waters, as a rule, tend to show increased levels of nutrients due to the production activities of biotas confined at shallow depths.

CONCLUSIONS

1. The geomorphological complexity of the islands investigated greatly affects oceanographic processes in their immediate vicinity.

2. Regions of the outer reef slopes are the most hydrodynamically active. Current speeds in these habitats can reach tens of centimeters per second, and separate short-term flow pulses can exceed $1 \text{ m}\cdot\text{sec}^{-1}$. The most intensive processes of turbulent exchange ($A_{\text{max}} = 10^4\text{-}10^7 \text{ cm}^2\cdot\text{sec}^{-1}$) also occur here. Reef platforms with typically rugose reliefs reduce current speeds both in the water column and near the bottom. Mean current speeds in subsurface layers of outer reef slopes are $30\text{-}40 \text{ cm}\cdot\text{sec}^{-1}$ ($A_{\text{max}} = 10^3\text{-}10^4 \text{ cm}^2\cdot\text{sec}^{-1}$), and near the bottom currents seldom exceed $5\text{-}10 \text{ cm}\cdot\text{sec}^{-1}$ ($A_{\text{max}} = 10^2\text{-}10^3 \text{ cm}^2\cdot\text{sec}^{-1}$).

Coastal wave currents with speeds up to $50 \text{ cm}\cdot\text{sec}^{-1}$ and exchange processes in the range of $10^5\text{-}10^6 \text{ cm}^2\cdot\text{sec}^{-1}$ may appear here (e.g., Desroches). In contrast, typical current speeds for coastal shallows protected from wind and waves are $2\text{-}4 \text{ cm}\cdot\text{sec}^{-1}$ ($A_{\text{max}} = 10^2\text{-}10^5 \text{ cm}^2\cdot\text{sec}^{-1}$). Narrowing of channels, which appears in the sedimentary locations of reefs and banks near Mahé Island and St. Joseph Atoll, promotes an increase of water exchange over the reef slope, with current speeds being $20\text{-}30 \text{ cm}\cdot\text{sec}^{-1}$ ($A_{\text{max}} = 10^4\text{-}10^6 \text{ cm}^2\cdot\text{sec}^{-1}$). Water movement in atoll lagoons depends on the proximity of channels exchanging of water during a tidal cycle. In sites having the most intensive flows, mean current speeds may reach $15\text{-}20 \text{ cm}\cdot\text{sec}^{-1}$ ($A_{\text{max}} = 10^3\text{-}10^5 \text{ cm}^2\cdot\text{sec}^{-1}$), however, lagoons subjected to intensive sedimentation are characterized by weak currents with $2\text{-}5 \text{ cm}\cdot\text{sec}^{-1}$ speed ($A_{\text{max}} = 10^2 \text{ cm}^2\cdot\text{sec}^{-1}$).

3. The main causes of turbulence on reefs are periodic processes with typical periods from 2 to 12-24 h. This is most conspicuous during tidal cycles with 12 and 6 h periods. Near the larger islands (e.g., Mahé) and also in St. Joseph and Cosmoledo Atoll lagoons, the turbulent effects of winds (24 h period) can be observed. Vortices, presumably of orographic or resonance origin, have periods of 16-18 h, large scale weather fluctuations of 30-40 h are also found in atoll lagoons. High frequency current pulses (1-3 h) can be observed in almost all portions of a reef profile and are related to wind and wave effects.

4. In the Seychelles region, three water masses were distinguished: surface equatorial, surface south subtropical and intermediate south subtropical. The islands investigated can be conditionally subdivided into two groups: northern (Mahé, La Digue, Praslin, Desroches) and southern (Astove, Providence, Aldabra, Cosmoledo, Farquhar, Cœtivy). The salinity of the water mass surrounding the northern group remains lower than 35.04 ppt. Such differentiation of surface waters is correlated with the location of the south tropical frontal water boundary.

5. Hydrological conditions in coastal island waters with fringing and platform reefs (Mahé, La Digue, Praslin, African Banks, Desroches, Cœtivy) depend to a large extent on hydrological processes of the surrounding ocean waters. Waters overlying reef platforms have more uniform

thermohaline characteristics. On island slopes (Cœtivy, Cerf, Aldabra, Farquhar), upwelling of cold subsurface waters resulted in differences between surface and near bottom temperatures of 4-12°C in coastal areas. The influx of subsurface waters had a cyclic nature and its intensity depended on interactions between storm wind drift and tidal rhythm.

6. The nutrient study showed concentrations in the coastal zones of the Seychelles that are similar to coral reef areas. In the coastal zones, phosphate concentrations are somewhat higher than in the open ocean, and the amount of organic phosphorus is close to that of inorganic phosphorus if there is no additional influx of $P-PO_4$ from greater depth (Cœtivy, Providence), sewage input from land (Mahé) or organic phosphorus from excrement of birds inhabiting some of the islands (Astove, Cosmoledo). On the whole, as occurs on other tropical reefs, the quantity of nutrients in Seychelles waters is not great, with the presence of semi-enclosed nutrient exchanges accounting for much of the productivity of their ecosystems.

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Table 1. Characteristics of hydrological stations.

Station	Location	Coordinates	Date	Period of Observation	Horizon	Weather Condition
1	Cœtivy	= 7° 8.3' = 56° 15.2'	13-15/1/89	49	10	NW, W wind 4-25 m·sec ⁻¹
1	Cœtivy	= 7° 8.3' = 56° 15.2'	13-14/1/89	28	20	NW, W wind 6-10 m·sec ⁻¹
1	Cœtivy	= 7° 8.3' = 56° 15.2'	14-15/1/89	32	28.5	NW, W wind 4-25 m·sec ⁻¹
2	Cœtivy	= 7° 9' = 56° 17.9'	15-17/1/89	34	10	NW, W wind 3-13 m·sec ⁻¹
2	Cœtivy	= 7° 9' = 56° 17.9'	15-17/1/89	34	30	NW, W wind 3-13 m·sec ⁻¹
3	Cœtivy	= 7° 12' = 56° 11.3'	14-15/1/89	18	4.5	NW, W wind 1-10 m·sec ⁻¹
4	Farquhar	= 10° 11.2' = 51° 11.3'	20-23/1/89	68	20	NW, W wind 5-12 m·sec ⁻¹
5	Farquhar	= 10° 8.8' = 51° 11.6'	21-23/1/89	55	8.5	NW, W wind 6-8 m·sec ⁻¹
6	Farquhar	= 10° 8.9' = 51° 11.8'	21-22/1/89	29	17.5	NW, W wind 5-8 m·sec ⁻¹
7	Desroches	= 5° 40.4' = 53° 39.3'	6-10/2/89	102	20	NW, W, N wind 2-14 m·sec ⁻¹
7	Desroches	= 5° 40.4' = 53° 39.3'	6-8/2/89	58	24.5	NW, W, N wind 3-14 m·sec ⁻¹
8	Desroches	= 5° 41.7' = 53° 40.1'	7-8/2/89	17	4.5	NW, W wind 3-14 m·sec ⁻¹
9	Desroches	= 5° 41.2' = 56° 39.8'	9-10/2/89	21	4.5	NW wind 3-8 m·sec ⁻¹
10	Praslin	= 4° 22.6' = 55° 44.2'	11-13/2/89	45	15	calm, NW, W wind 2-4 m·sec ⁻¹
11	Praslin	= 4° 21.4' = 55° 45.8'	11-13/2/89	46	9.5	calm, NW, W wind 2-4 m·sec ⁻¹

Table 1. Continued.

Station	Location	Coordinates	Date	Period of Observation	Horizon	Weather Condition
12	Mahé	= 4° 36.36' = 55° 28.5'	15-24/2/89	206	9.5	NW, W wind 2-8 m·sec ⁻¹
13	Mahé	= 4° 37.42' = 55° 29.22'	15-20/2/89	118	3.5	NW, W wind 2-8 m·sec ⁻¹
14	African	= 4° 55.9' = 53° 23.6'	27-28/2/89	24	16	NW wind 2-5 m·sec ⁻¹
15	St. Joseph	= 5° 27.7' = 53° 23.6'	2-4/3/89	49	15	NW, N wind 2-7 m·sec ⁻¹
16	St. Joseph	= 5° 24.64' = 53° 19.04'	1-4/3/89	71	26.5	NW, N wind 2-7 m·sec ⁻¹
17	St. Joseph	= 5° 24.92' = 53° 19.35'	1-4/3/89	68	2.5	NW, N wind 2-7 m·sec ⁻¹
18	Cosmoledo	= 9° 44.9' = 47° 39.5'	7-9/3/89	43	12	E, NE wind 2-15 m·sec ⁻¹
19	Cosmoledo	= 9° 44.9' = 47° 39.5'	7-9/3/89	50	11.5	E, NE wind 2-15 m·sec ⁻¹
20	Cosmoledo	= 9° 43.62' = 47° 37.23'	7-9/3/89	57	2.5	E, NE wind 2-15 m·sec ⁻¹
21	Aldabra	= 9° 25' = 46° 32'	27-28/2/89	30	20	N, NW wind 2-5 m·sec ⁻¹

Table 2. Current parameters and characteristics of horizontal turbulent exchange in the studied areas. y/W_y = current direction (in degrees) / density of direction probability. V/W_v = current speed ($\text{cm}\cdot\text{sec}^{-1}$) / density of rate probability. $J_{u,v}$ = mean turbulent intensity for speed vector components. α = direction of maximal turbulent exchange, in degrees. $\epsilon = A_{\max}/A_{\min}$ - index of anisotropy of turbulent exchange.

Station	Horizon, m	y/W_y	V/W_v	J_v	J_u	A_{\max}	α	ϵ
1	10	<u>25-30</u> 0.02 <u>55-60</u> 0.01	<u>10-14</u> 0.05 <u>15-19</u> 0.04	0.35 ± 0.26	0.39 ± 0.27	$177 \cdot 10^3 \pm 14 \cdot 10^3$	57	9.9
1	20	<u>50-54</u> 0.02	<u>15-24</u> 0.01	0.48 ± 0.35	0.51 ± 0.35	$225 \cdot 10^3 \pm 25 \cdot 10^3$	59	9.5
1	28.5	<u>135-140</u> 0.01	<u>2-4</u> 0.2	1.39 ± 0.74	1.23 ± 0.78	$2 \cdot 10^3 \pm 0.2 \cdot 10^3$	85	7.7
2	10	<u>30-40</u> 0.02	<u>2-4</u> 0.05 <u>15-19</u> 0.02	0.51 ± 0.37	0.47 ± 0.36	$500 \cdot 10^3 \pm 81 \cdot 10^3$	70	7.0
2	30	<u>35-50</u> 0.02	<u>25-30</u> 0.02	0.94 ± 0.31	0.89 ± 0.24	$903 \cdot 10^3 \pm 533 \cdot 10^3$	75	10.0
3	4.5	<u>285-295</u> .01-.02	<u>15-19</u> 0.02	2.57 ± 1.94	1.71 ± 0.77	$604 \cdot 10^3 \pm 168 \cdot 10^3$	84	22.7
4	20	<u>15-20</u> 0.02 <u>195-200</u> 0.02	<u>25-30</u> 0.02 <u>40-50</u> 0.02 <u>60-65</u> 0.01	0.78 ± 0.52	0.69 ± 0.48	$1154 \cdot 10^3 \pm 101 \cdot 10^3$	71	5.6
5	8.5	<u>340-350</u> 0.01	<u>2-9</u> .06-.09	1.07 ± 0.76	0.88 ± 0.94	$27 \cdot 10^3 \pm 4 \cdot 10^3$	84	4.6
6	17.5	<u>20-30</u> 0.02 <u>200-215</u> 0.014	<u>2-4</u> 0.004	1.29 ± 0.89	1.07 ± 1.33	$15 \cdot 10^3 \pm 0.6 \cdot 10^3$	91	8.7
7	20	<u>50-55</u> 0.08 <u>245-250</u> 0.08	<u>10-15</u> 0.004	6.57 ± 11.68	6.27 ± 7.77	$11 \cdot 10^3 \pm 4.6 \cdot 10^3$	76	11.4
7	24.5	<u>125-129</u> 0.01	<u>2-4</u> 0.13	1.29 ± 0.89	0.82 ± 0.61	$8 \cdot 10^3 \pm 1.1 \cdot 10^3$	103	9.4

Table 2. Continued

Station	Horizon, m	y/W_y	V/W_v	J_v	J_u	A_{\max}	α	ϵ
8	4.5	<u>80-90</u> 0.06 <u>145-150</u> 0.01	<u>20-24</u> 0.07	1.66 ± 1.21	1.19 ± 0.72	$504 \cdot 10^3 \pm$ $105 \cdot 10^3$	81	7.7
9	4.5	<u>45-50</u> 0.03	<u>2-4</u> 0.2	0.12 ± 0.22	0.48 ± 1.79	$31 \cdot 10^3 \pm$ $26 \cdot 10^3$	54	397.4
10	15	<u>100-110</u> 0.01 <u>300-305</u> 0.08	<u>10-14</u> 0.04 <u>20-24</u> 0.05	36 ± 0.26	0.50 ± 0.34	$120 \cdot 10^3 \pm$ $15 \cdot 10^3$	121	7.7
11	9.5	<u>300-304</u> 0.08	<u>2-4</u> 0.2	9.40 ± 4.99	8.5 ± 3.1	$3 \cdot 10^3 \pm$ $0.3 \cdot 10^3$	91	5.5
12	9.5	<u>270-275</u> .01-.02	<u>15-19</u> 0.1	1.35 ± 1.10	1.13 ± 0.84	$199 \cdot 10^3 \pm$ $10 \cdot 10^3$	116	7.0
13	3.5	<u>60-80</u> .015-.016	<u>15-20</u> 0.06	0.42 ± 0.36	0.50 ± 0.29	$161 \cdot 10^3 \pm$ $11 \cdot 10^3$	54	6.5
14	16	<u>95-100</u> 0.02	<u>15-19</u> 0.04 <u>25-30</u> 0.03	1.20 ± 0.53	0.82 ± 0.45	$407 \cdot 10^3 \pm$ $61 \cdot 10^3$	83	9.1
15	15	<u>55-65</u> 0.011 <u>215-220</u> 0.010	<u>20-24</u> 0.03 <u>40-45</u> 0.03	0.51 ± 0.27	0.58 ± 0.24	$89 \cdot 10^3 \pm$ $10 \cdot 10^3$	79	5.8
16	26.5	<u>5-15</u> 0.03 <u>195-200</u> 0.02	<u>2-4</u> 0.10 <u>10-15</u> 0.02	0.31 ± 0.24	0.70 ± 0.58	$10 \cdot 10^3 \pm$ $3 \cdot 10^3$	65	17.9
17	2.5	<u>275-280</u> 0.02 <u>330-335</u> 0.02	<u>2-4</u> 0.17	0.15 ± 0.26	0.10 ± 0.11	$0.8 \cdot 10^3 \pm$ $0.3 \cdot 10^3$	60	20.4
18	12	<u>75-80</u> 0.006 <u>205-210</u> 0.01	<u>5-10</u> 0.04 <u>30-34</u> 0.04	0.74 ± 0.38	0.67 ± 0.36	$126 \cdot 10^3 \pm$ $17 \cdot 10^3$	80	9.6

Table 2. Continued

Station	Horizon, m	y/W_y	V/W_v	J_v	J_u	A_{\max}	α	ϵ
19	11.5	<u>175-180</u> 0.01 <u>215-220</u> 0.01	<u>20-29</u> 0.10	1.29 ± 0.58	1.13 ± 0.68	$286 \cdot 10^3 \pm$ $32 \cdot 10^3$	104	6.1
20	2.5	<u>5-9</u> 0.02 <u>180-195</u> 0.03	<u>5-10</u> 0.06	0.43 ± 0.27	1.04 ± 0.76	$17 \cdot 10^3 \pm$ $4 \cdot 10^3$	57	15.5
21	20	<u>350-355</u> 0.02	<u>2-4</u> 0.15 <u>55-70</u> 0.03	0.22 ± 0.31	0.20 ± 0.36	$38 \cdot 10^3 \pm$ $1.3 \cdot 10^3$	64	10.2

Table 3. Concentration of nutrients in surface waters of the Seychelles Islands (January - March, 1989). n = number of samples taken.

Island	n	$\mu\text{g-atom}\cdot\text{l}^{-1}$				n				
		phosphate	organic phosphorus	silicon			nitrites	ammonia	nitrates	organic nitrogen
Cœtivy coastal ocean	10	0.46±0.21	0.15±0.12	3.74±1.32	6	0.32±0.13	1.09±1.06	3.35±4.10	28.48±20.8	
	6	0.25±0.05	0.12±0.11	2.90±0.26	2	0-0.34	0-0.42	0-0.48	7.1-13.1	
Farquhar coastal ocean lagoon	3	0.27±0.09	0.23±0.17	2.42±0.79	2	0.13±0.14	0.05±0.07	0.1±0.14	7.45±3.61	
	4	0.22±0.04	0.13±0.04	2.29±0.16	1	0.17	0	1.2	-	
	3	0.36±0.18	0.06±0.07	3.23±0.25	3	0.10±0.02	1.43±0.67	1.6±0.85	26.5±2.33±	
Aldabra coastal ocean lagoon	3	0.21±0.04	0.22±0.06	2.16±0.39	3	0.05±0.16	0.54±0.16	1.36±0.25	18.37±2.22	
	4	0.20±0.07	0.16±0.04	2.08±0.19	1	0	0	0.11	15.9	
	6	0.20±0.03	0.12±0.04	1.91±0.36	3	0.02±0.03	0.30±0.12	1.26±0.18	16.67±3.71	
Desroches coastal lagoon coastal ocean central lagoon	6	0.24±0.11	0.11±0.04	2.49±0.37	4	0.08±0.02	0.63±0.48	0.6±0.66	14.13±1.91	
	6	0.25±0.13	0.12±0.09	2.79±0.87	5	0.03±0.04	0	0.35±0.32	13.36±2.54	
	7	0.20±0.07	0.17±0.07	2.30±0.12	1	0.04	0.02	0.11	7.5	
African Banks coastal ocean	3	0.14±0.06	0.32±0.04	1.37±0.08	3	0	1.07±0.92	0.11±0.05	10.3±4.97	
	5	0.14±0.05	0.19±0.11	1.70±0.48	5	0.76±1.70	0.76±1.70	0.09±0.05	7.6±3.1	
St.Joseph coastal ocean lagoon	5	0.14±0.06	0.16±0.05	1.5±0.19	5	0	0.48±0.53	0.78±0.19	8.83±0.29	
	5	0.17±0.06	0.18±0.07	1.79±0.19	5	0	0.41±0.54	0.52±0.04	10.78±3.7	
	2	0.09±0.04	0.33±0.12	1.68±0.04	2	0	0.5	0.76±0.09	7.8±2.12	
Providence coastal ocean	4	0.24±0.04	0.21±0.04	1.90±0.06	4	0	0.17±0.22	0.59±0.16	16.83±4.9	
	2	0.21±0.08	0.23±0.13	2.44±0.06	2	0	0	0.88±0.40	17.45±1.7	
Cosmoledo coastal ocean lagoon	1	0.21	1.48	2.15	2	0.27±0.38	0.27±0.38	0.44±0.02	9.5±4.95	
	4	0.13±0.03	0.85±0.77	2.16±0.26	4	0	0.27±0.14	0.45±0.04	17.63±6.5	
	7	0.25±0.17	0.81±0.26	2.34±0.26	7	0	0.33±0.40	0.57±0.18	17.28±2.8	

Table 3. Continued

Island	n	phosphate	organic phosphorus	silicon	n	nitrites	ammonia	nitrates	organic nitrogen
Astove									
coastal	1	0.23	0.16	1.8	1	0	0.94	0.95	-
ocean	3	0.20±0.05	0.29±0.13	2.20±0.65	3	0	0.41±0.81	0.58±0.25	9.17±1.21
lagoon	2	0.13±0.04	0.73±0.05	1.21±0.79	2	0	0.73±0.77	0.44±0.02	8.3±2.55
Mahé									
coastal	9	0.24±0.09	0.11±0.06	2.31±0.53	6	0.09±0.05	0.52±0.79	0.21±0.23	12.12±6.6
Praslin									
coastal	3	0.10±0.03	0.2±0.01	2.11±0.42	1	0	3.1	0.3	8.4
ocean	4	0.14±0.02	0.2±0.03	2.30±0.2	2	0	0-1.0	0.0-0.6	11.22-15.1
La Digue									
coastal	3	0.17±0.08	0.15±0.1	2.05±0.14	4	0	0.19±0.24	0.25±0.2	8.97±3.56
ocean	1	0.08	0.16	1.97	1	0	0	0.0	11.9

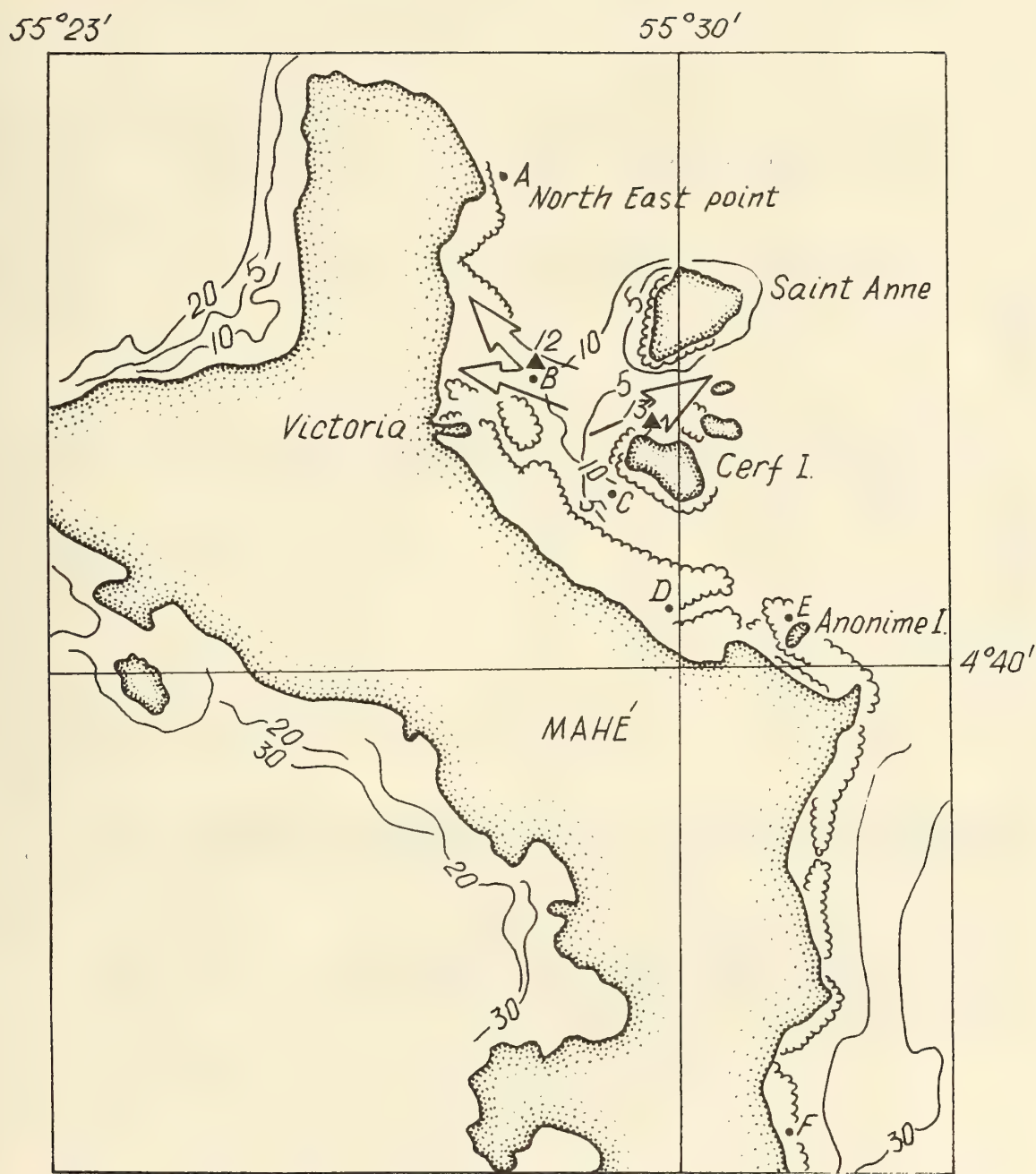


Figure 1. Scheme of hydrological stations at Mahé.

Designations:

- ▲ - subsurface currents
- ⋯ - near-bottom currents
- - stations with full complex of hydrological observations
- * - stations of underwater light measurements
- - hydrochemical sections
- ▲ - stations of near-bottom current measurements

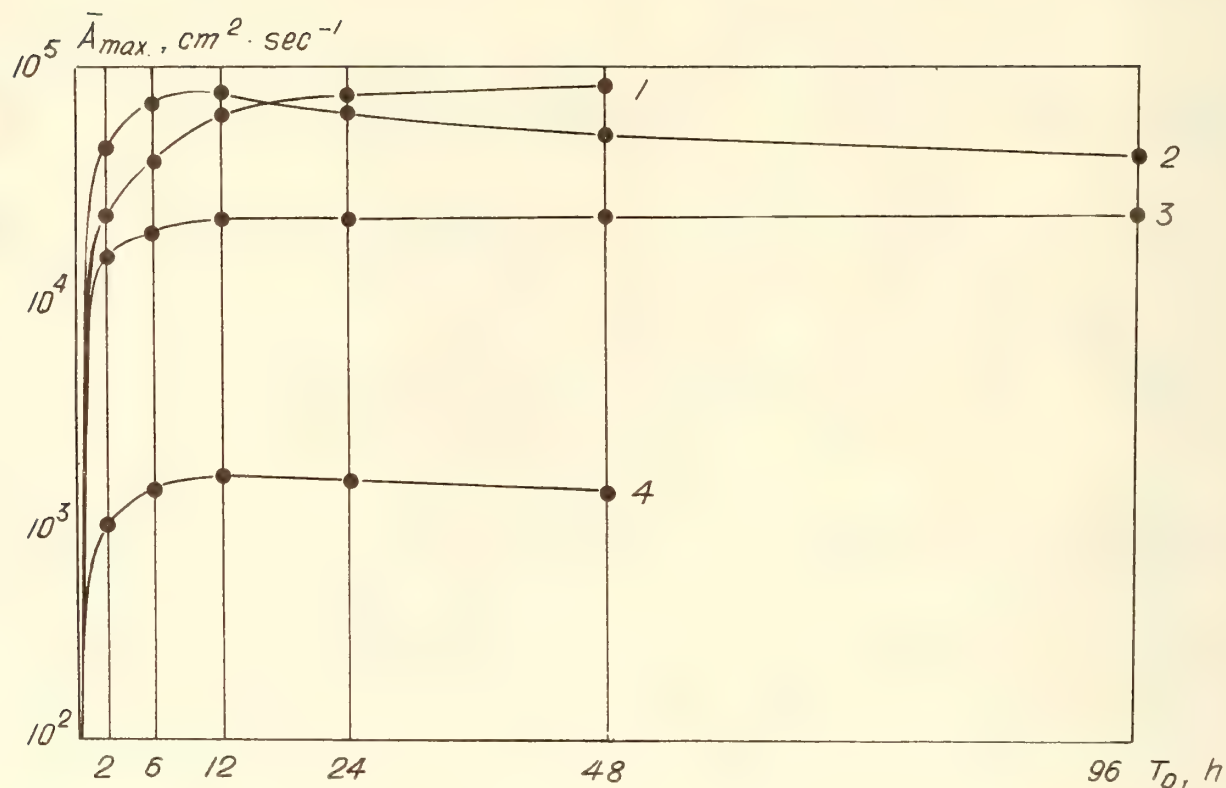


Figure 2. Change of mean maximal coefficients of horizontal turbulent exchange of motion quantity (\bar{A}_{max}) with the increase of averaging period (T_0) at granite islands:

- 1 - south coast of Praslin, station 10, horizon 15 m, depth of 23 m.
- 2 - northeastern coast of Mahé, anchorage in port, station 12, horizon 9.5 m, depth of 10 m.
- 3 - northeastern coast of Mahé, station 13, horizon 3.5m, depth of 4 m.
- 4 - south coast of Praslin, station 11, horizon 9.5 m, depth of 10 m.

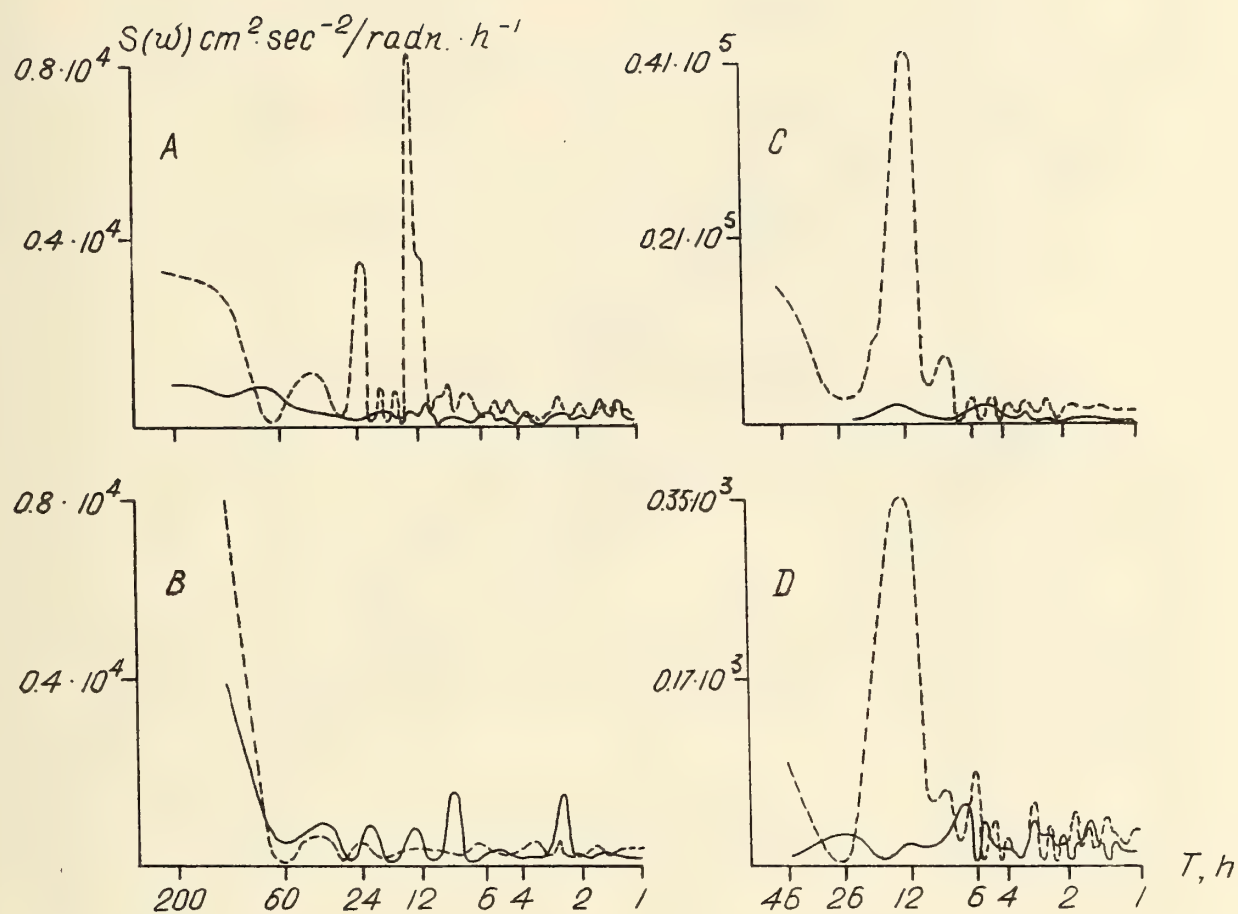


Figure 3. Functions of spectral density of current rate pulse at granitic islands:

A - northeastern coast of Mahé, anchorage in the port, station 12, horizon 9.5 m, depth 10 m.

B - northeastern coast of Mahé, shallow at the Cerf Is., horizon 3.5 m, depth of 4 m.

C - south coast of Praslin, station 10, horizon 15 m, depth of 23 m.

D - south coast of Praslin, station 11, horizon 9.5 m, depth of 10 m.

Continuous line shows the function for meridional component of current speed vector, interrupted one - for a zonal component.

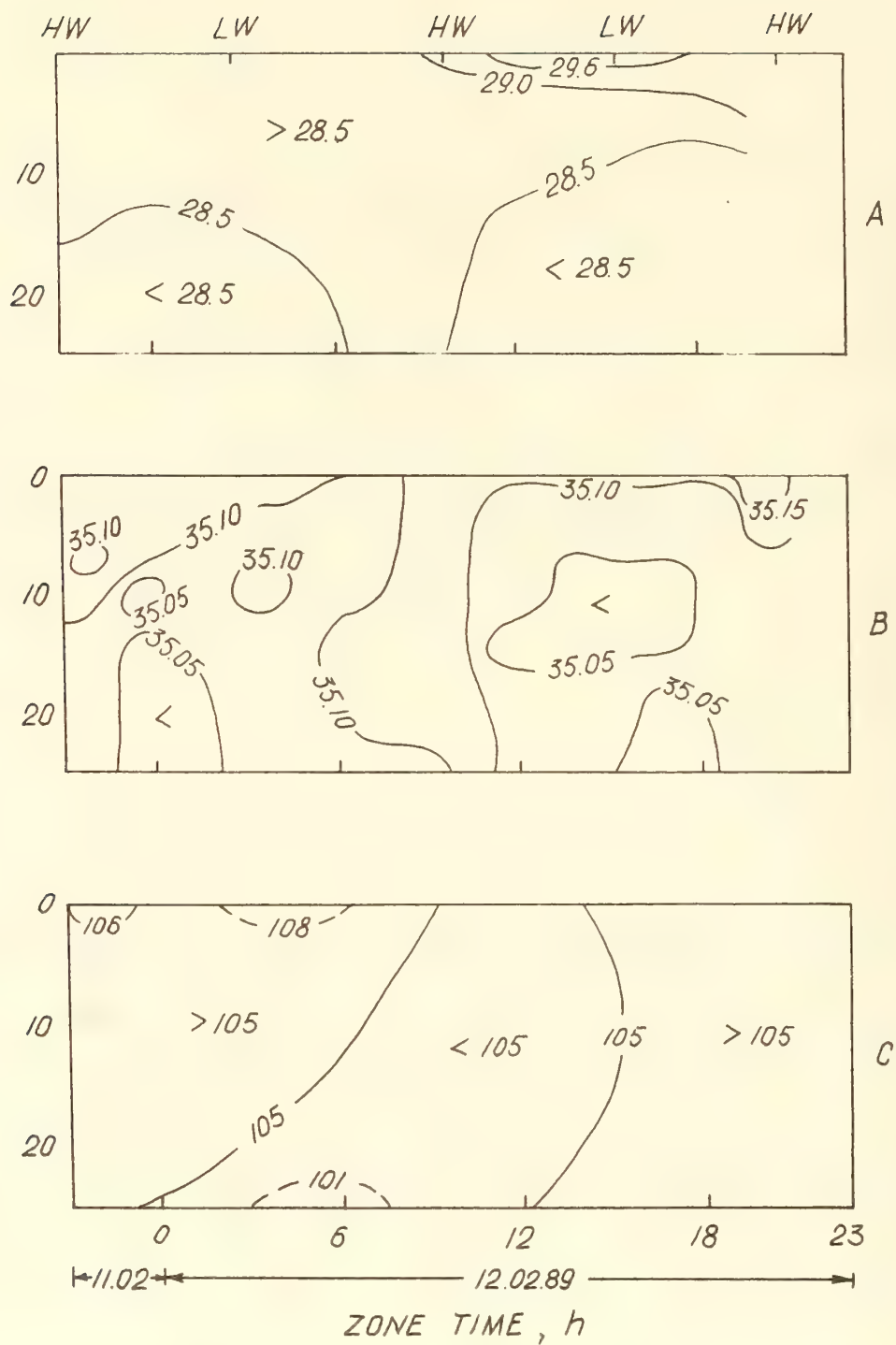


Figure 4. Fluctuations of temperature (A), salinity (B) and dissolved oxygen concentration (C) at Praslin.

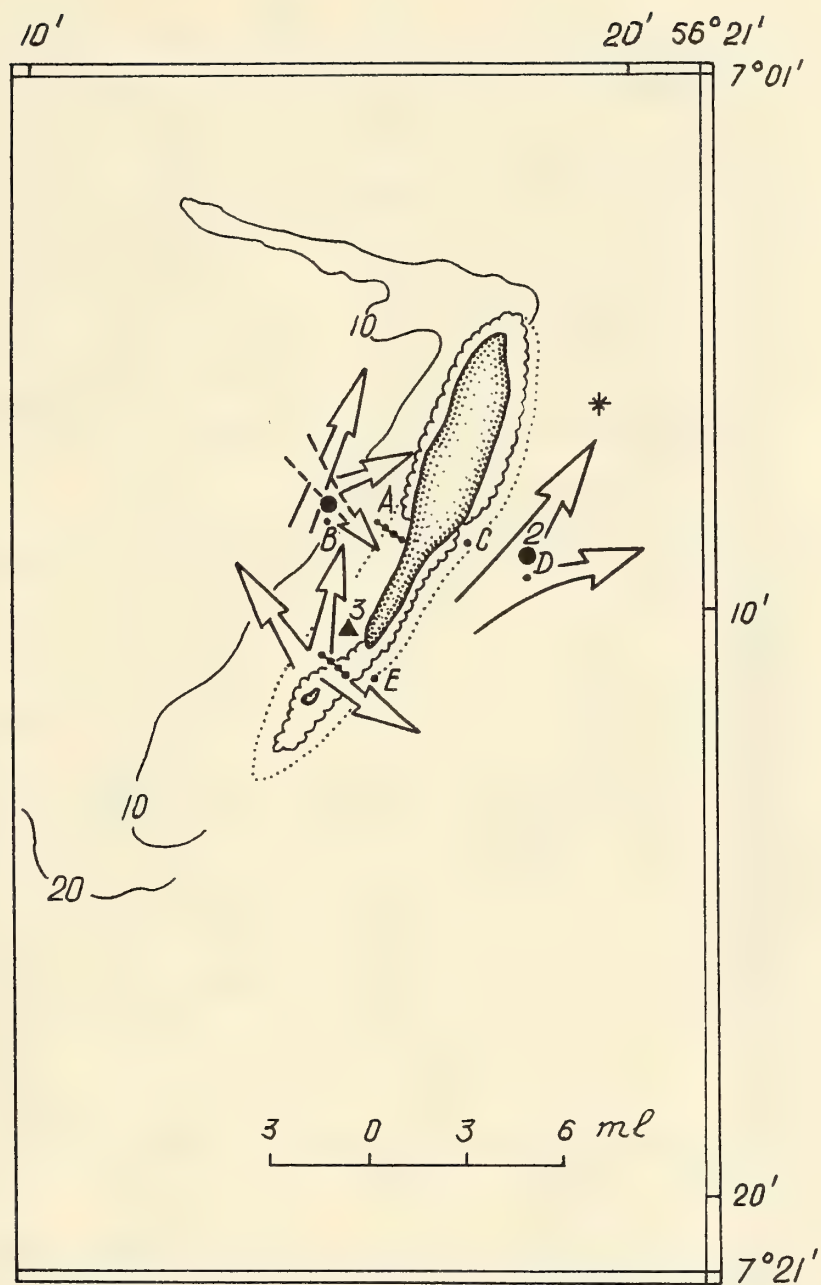


Figure 5. Scheme of hydrological stations and currents at Cöetivy.

Designations:

- ▲ - subsurface currents
- ▲ - near-bottom currents
- - stations with full complex of hydrological observations
- * - stations of underwater light measurements
- - hydrochemical sections
- ▲ - stations of near-bottom current measurements

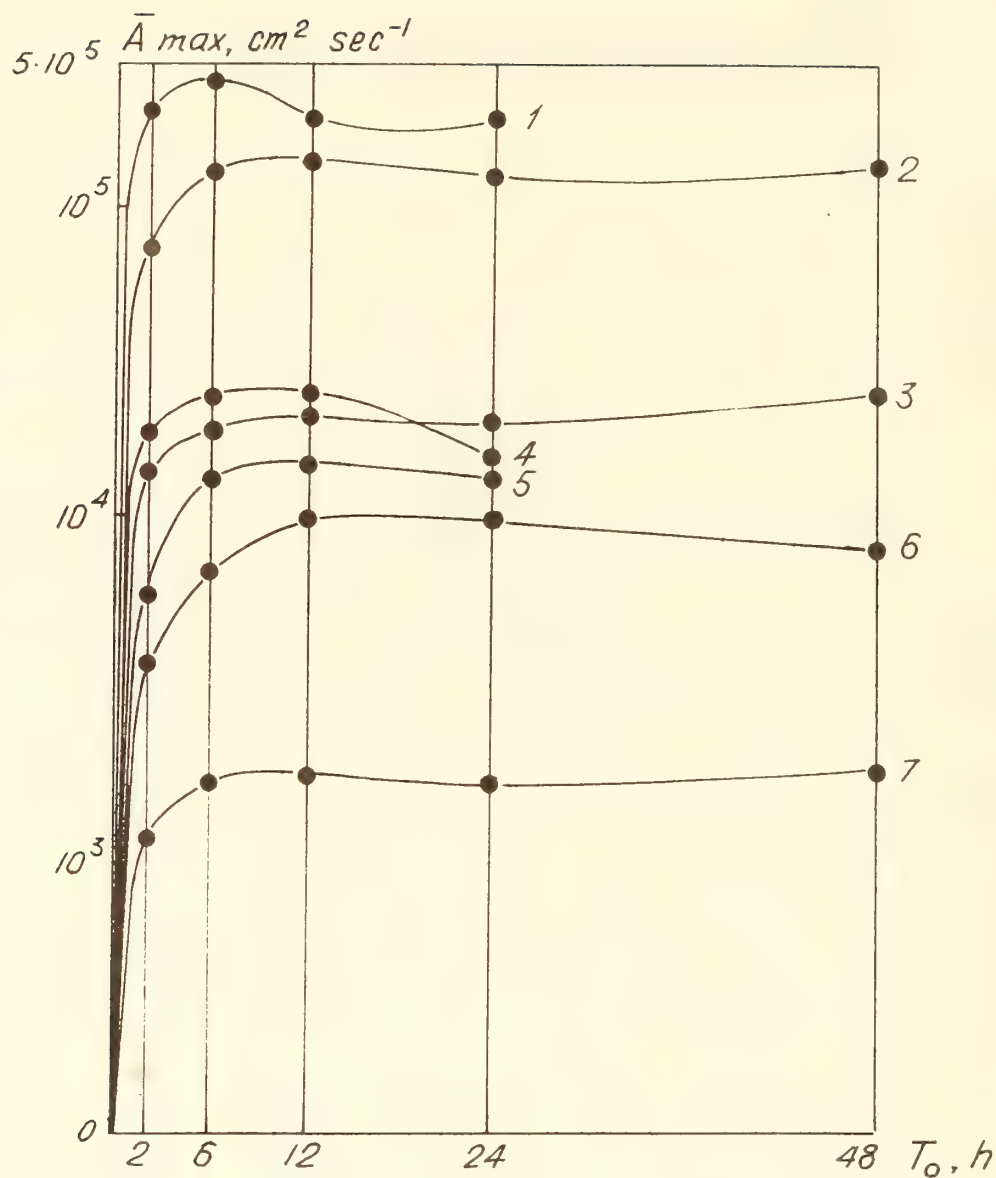


Figure 6. Fluctuations of averaged maximal coefficients of horizontal turbulent exchange of motion quantity (A_{max}) caused by the increase of averaging period (T_o) at Cöetivy.

- 1 - northwestern coast, station 8, horizon 4.5 m, depth of 5 m.
- 2 - eastern coast, station 2, horizon 30 m, depth of 50 m.
- 3 - eastern coast, station 2, horizon 10 m, depth of 50 m.
- 4 - western coast, station 3, horizon 4.5 m, depth of 5 m.
- 5 - western coast, station 1, horizon 4.5 m, depth of 29 m.
- 6 - western coast, station 1, horizon 10 m, depth of 29 m.
- 7 - western coast, station 1, horizon 8.5 m, depth of 29 m.

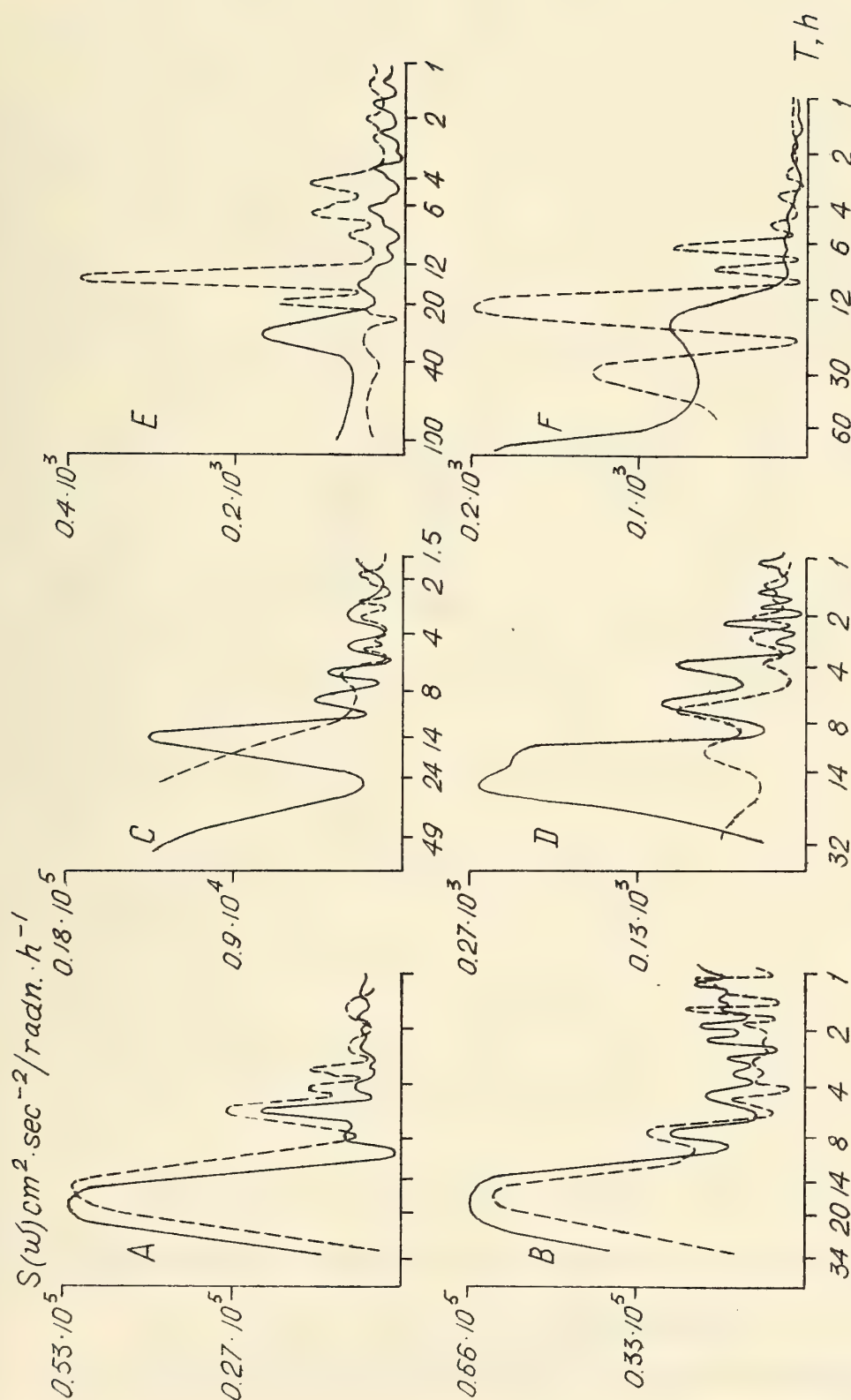


Figure 7. Functions of spectral density of current rate pulse at coral islands.

- A - Cœtivy, east coast, station 2, horizon 10 m, depth of 50 m.
 B - Cœtivy, east coast, station 2, horizon 30 m, depth of 50 m.
 C - Cœtivy, west coast, station 1, horizon 10 m, depth of 29 m.
 D - Cœtivy, west coast, station 1, horizon 28.5 m, depth of 29 m.
 E - Desroches, northwestern coast, station 7, horizon 20 m, depth of 25 m.
 F - Desroches, northwestern coast, station 7, horizon 24.5 m, depth of 25 m.

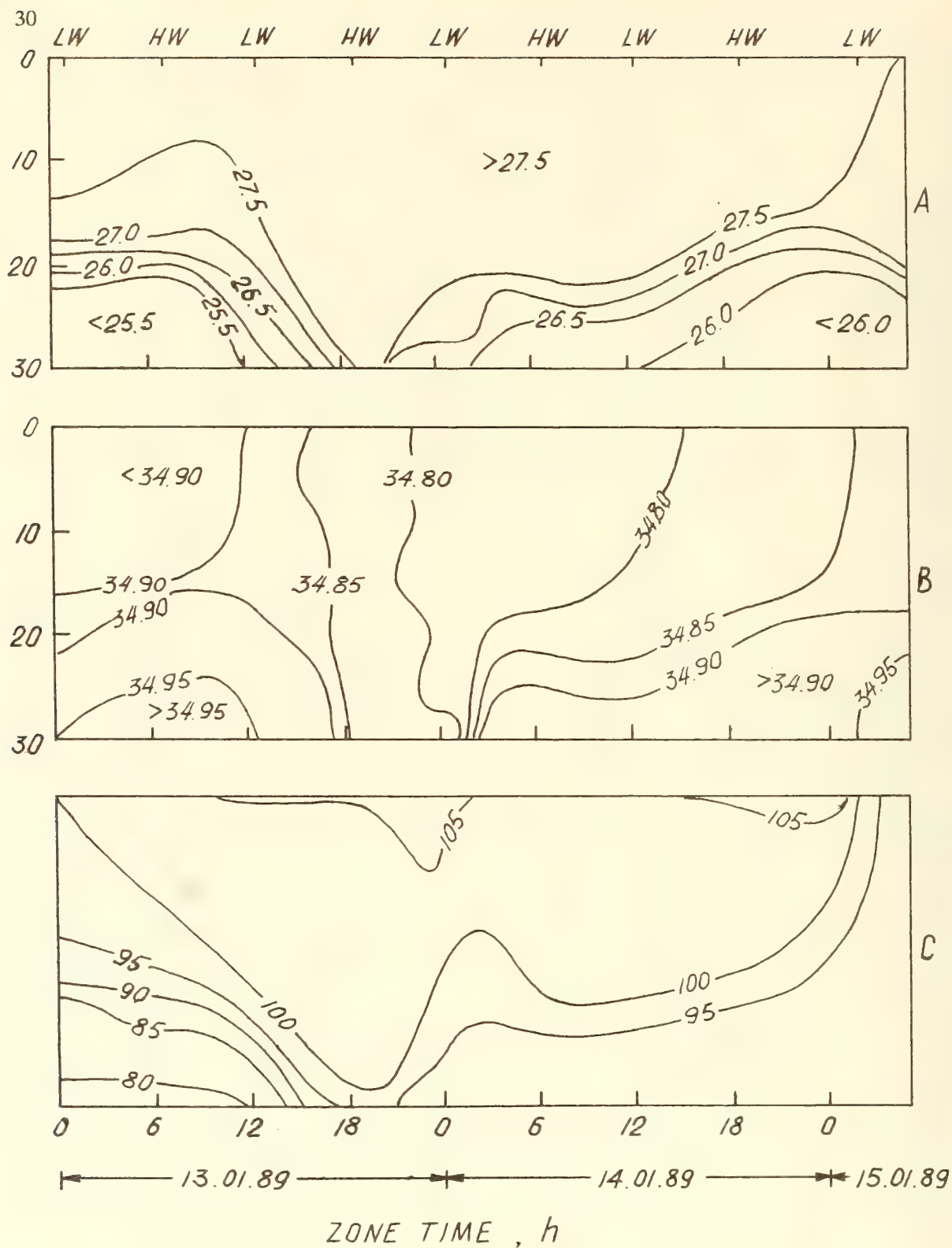


Figure 8. Temporal variability of temperature (A), salinity (B) and dissolved oxygen concentration (C) at Station 1, Cöetivy.

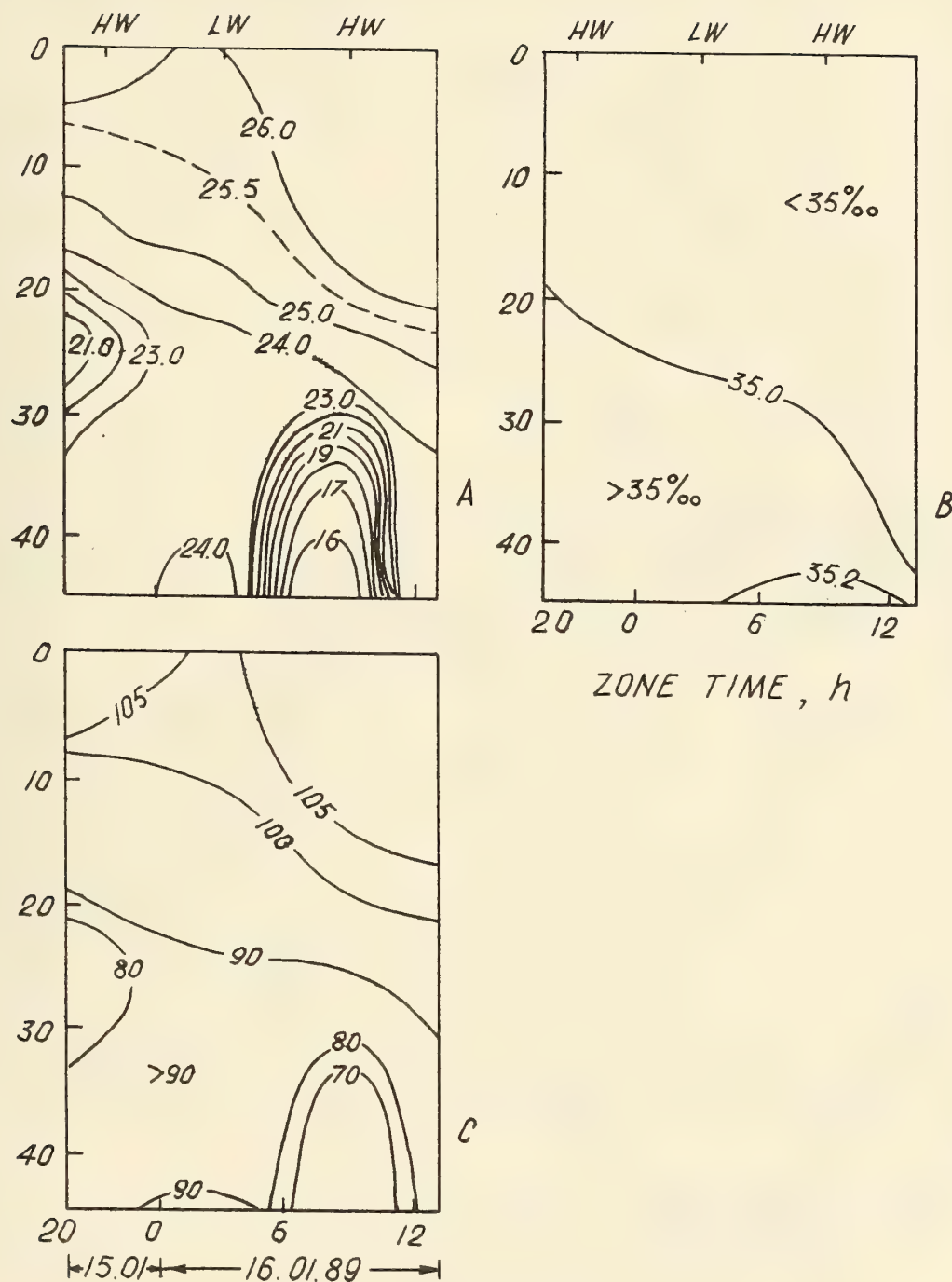


Figure 9. Temporal variability of temperature (A), salinity (B) and dissolved oxygen concentration (C) at Station 2, Cöetiv.

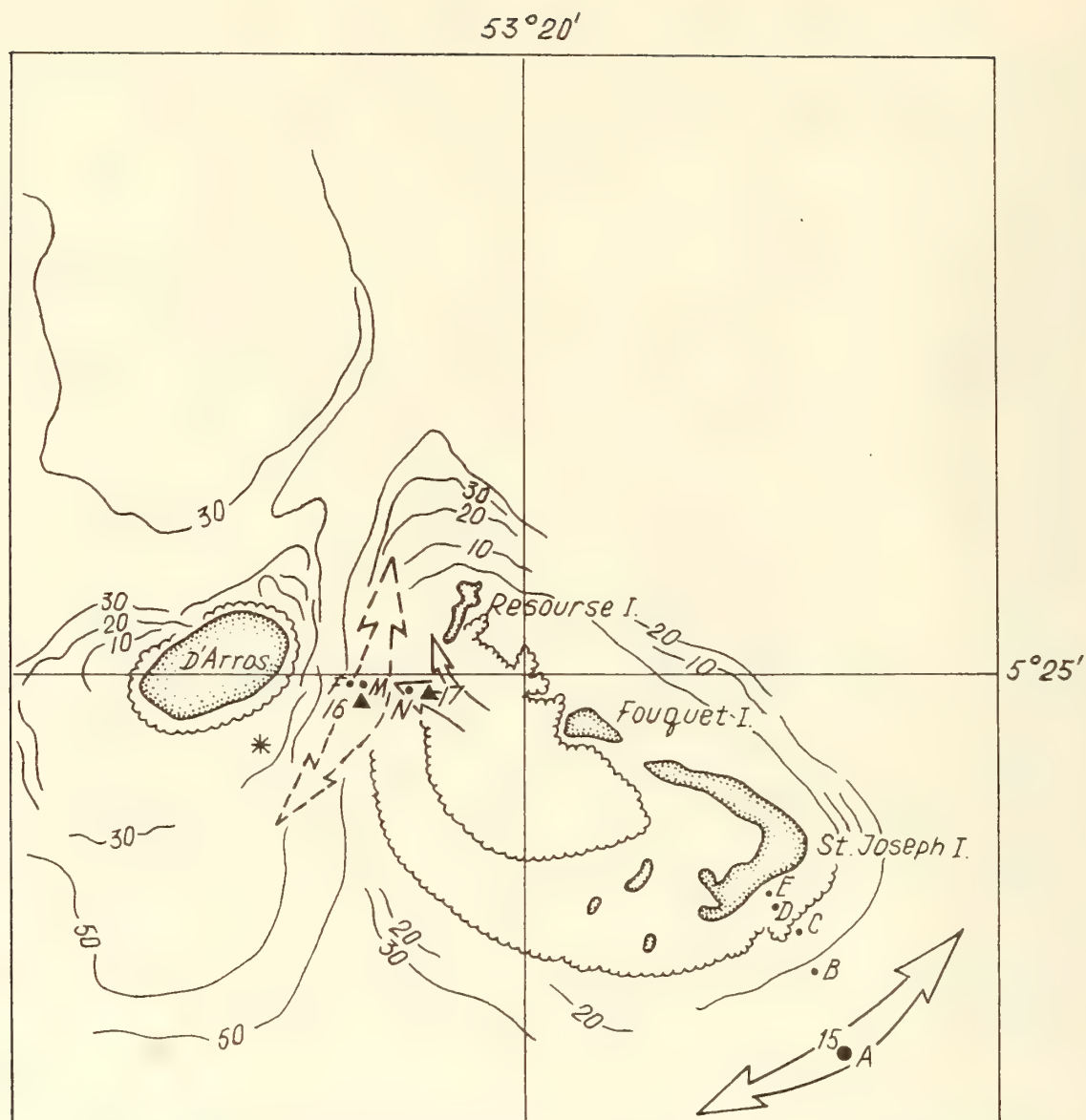


Figure 10. Scheme of hydrological stations and currents at western (A) and eastern (B) coasts of St. Joseph.

Designations:

- ▲ - subsurface currents
- ▲ - near-bottom currents
- - stations with full complex of hydrological observations
- * - stations of underwater light measurements
- - hydrochemical sections
- ▲ - stations of near-bottom current measurements

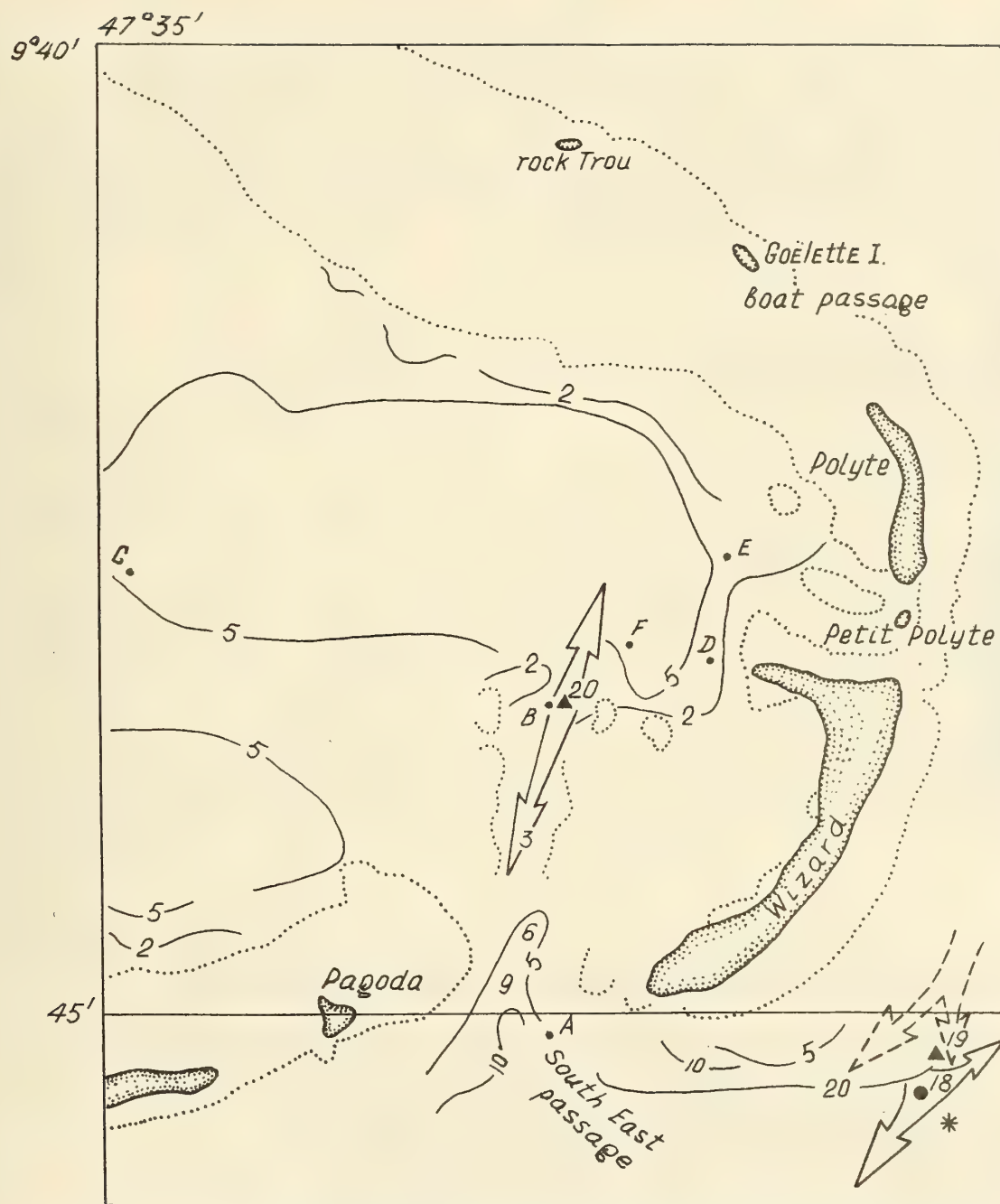


Figure 11. Scheme of hydrological stations and currents at southeastern coast of Cosmoledo.

Designations:

- ↗ - subsurface currents
- ↘ - near-bottom currents
- - stations with full complex of hydrological observations
- * - stations of underwater light measurements
- - hydrochemical sections
- ▲ - stations of near-bottom current measurements

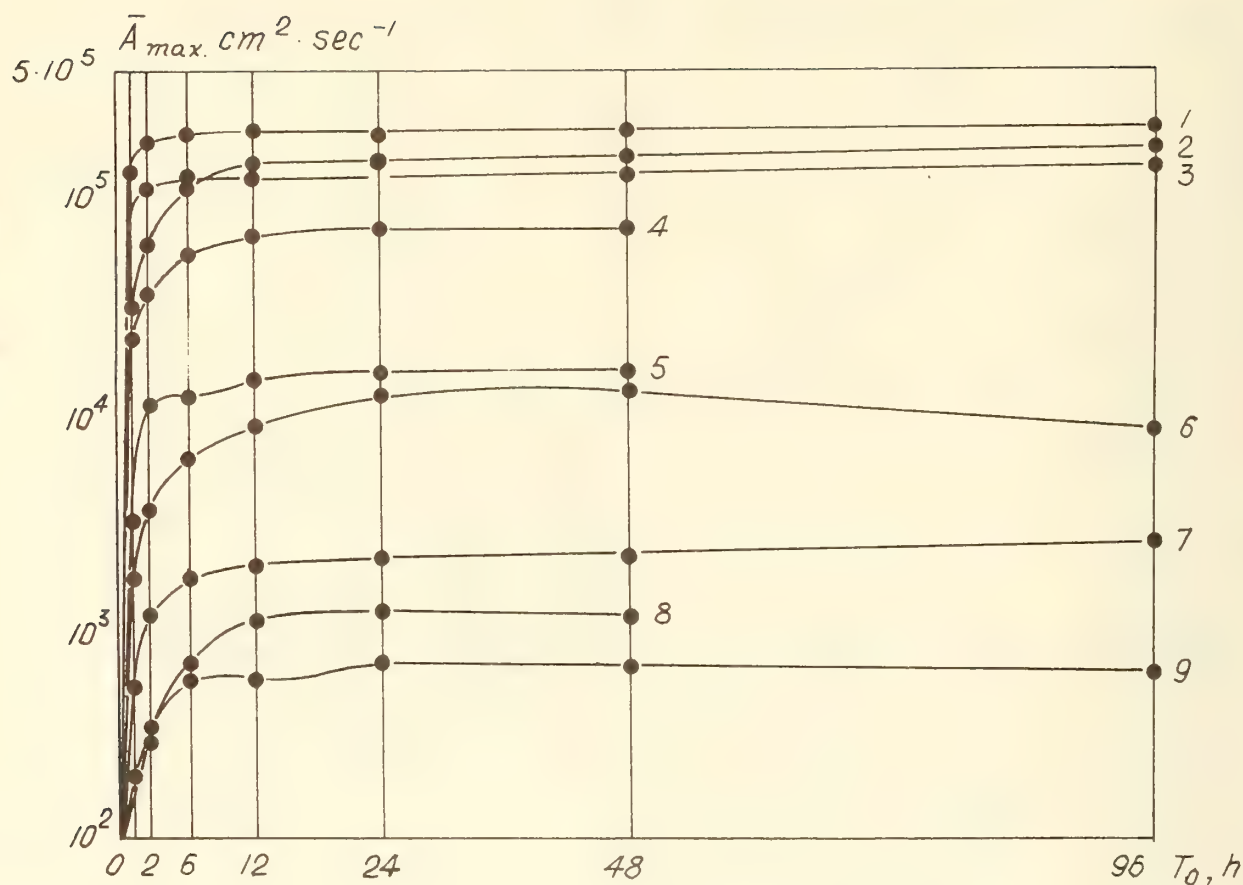


Figure 12. Fluctuations of averaged maximal coefficients of horizontal turbulent exchange of motion quantity (\bar{A}_{max}) due to the increase of averaging period (T_0) at atolls.

- 1 - southeastern coast of Cosmoledo, reef crest, station 19, horizon 11.5 m, depth of 12 m.
- 2 - southeastern coast of Cosmoledo, reef slope, station 18, horizon 12 m, depth of 20 m.
- 3 - eastern coast of Farquhar, station 4, horizon 20 m, depth of 50 m.
- 4 - southwestern coast of St. Joseph, station 15, horizon 15, depth of 32 m.
- 5 - Cosmoledo lagoon, at the Southeast Passage, station 20, horizon 2.5 m, depth of 3 m.
- 6 - western coast of St. Joseph, station 16, horizon 26.5 m, depth 27 m.
- 7 - eastern coast of Farquhar, station 6, horizon 17.5 m, depth of 18 m.
- 8 - eastern coast of Farquhar, station 5, horizon 8.5 m, depth 9 m.
- 9 - St. Joseph lagoon, station 17, horizon 2.2 m, depth of 3 m.

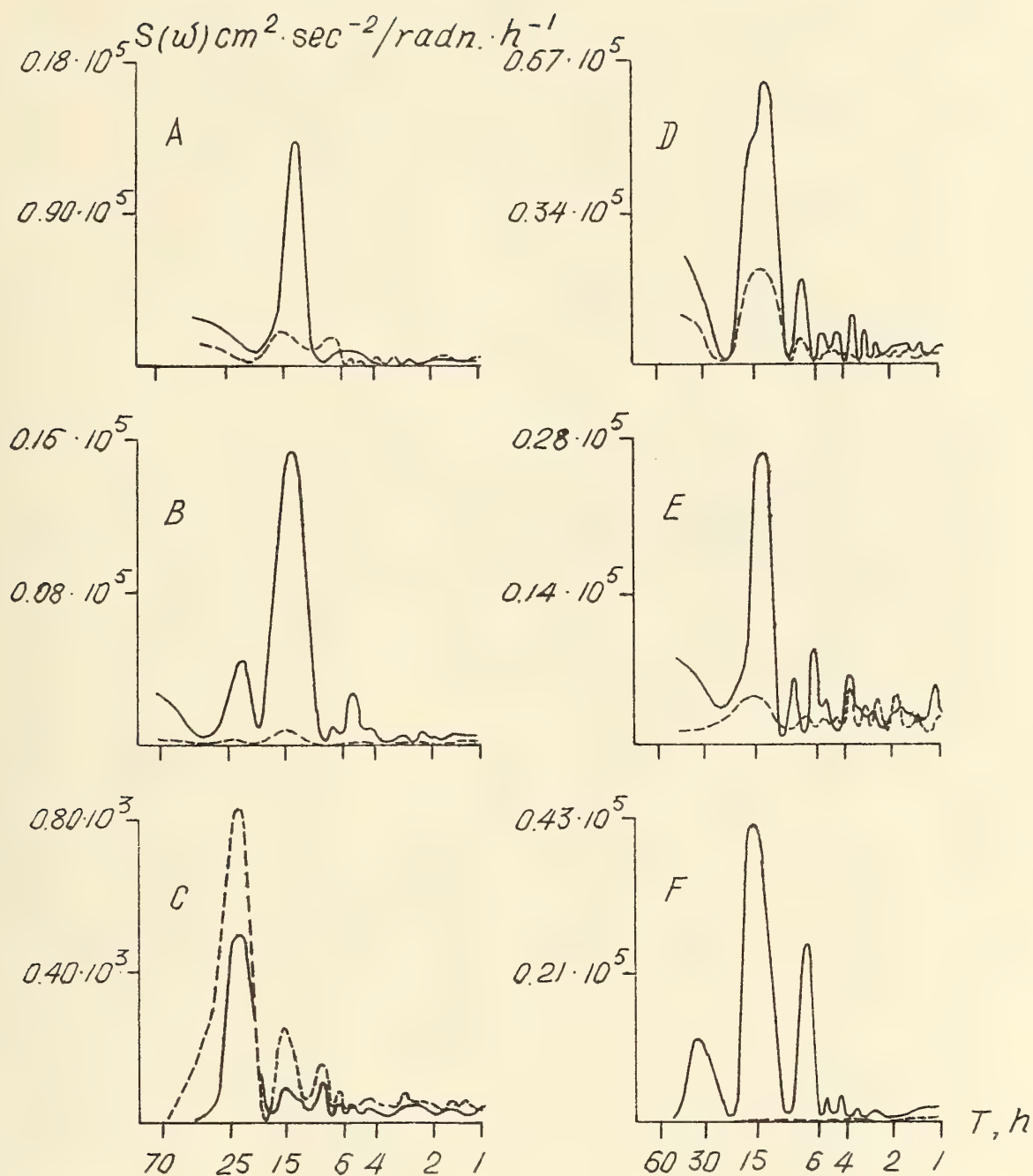


Figure 13. Function of spectral density of current rate pulse at atolls.

- A - reef slope at St. Joseph, station 15, horizon 15 m, depth 32 m.
- B - fore-reef platform at St. Joseph lagoon, station 16, horizon 26.5 m, depth of 27 m.
- C - St. Joseph lagoon, station 17, horizon 2.5 m, depth of 3 m;
- D - south-eastern coast of Cosmoledo, station 20, horizon 12 m, depth of 20 m;
- E - south-eastern coast of Cosmoledo, station 19, horizon 11.5 m, depth of 12 m;
- F - lagoon area adjoining Southeast Passage channel (Cosmoledo), station 20, horizon 2.5 m, depth of 3 m.

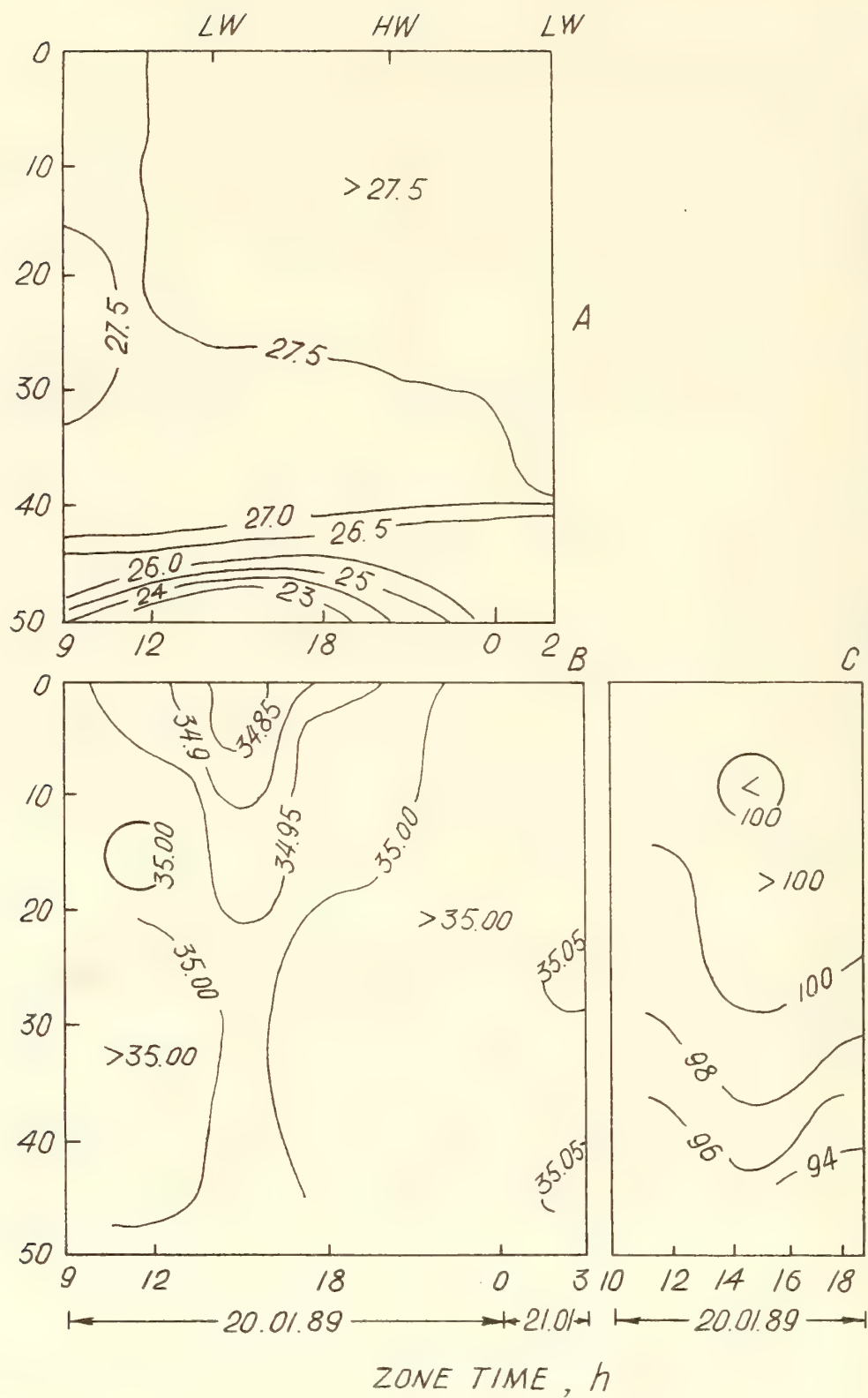


Figure 14. Temporal variability of temperature (A), salinity (B) and dissolved oxygen concentration (C) at Station 4, Farquhar.

CHAPTER 3

OCTOCORALLIA FROM THE SEYCHELLES ISLANDS

WITH SOME ECOLOGICAL OBSERVATIONS

BY

Andrey N. Malyutin*

INTRODUCTION

Octocorals are among the prominent components of reef communities of the Seychelles, but little faunistic information has been available (Thomson and Mackinnon 1910, Verseveldt 1976). Practically nothing is known about their vertical distribution on tropical reefs. This paper is a preliminary report on the identification of the octocoral collections made during the voyage of the R/V Akademik A. Nesmeyanov from January to March 1989, with some ecological observations. The following checklist presents a survey of the species collected during this voyage in addition to species recorded earlier.

LIST OF SPECIES

Order Helioporacea

Family Helioporacea

1. *Heliopora coerulea* (Pallas)(C  etivy, Aldabra, D'Arros, depth 5-13m)

Order Alcyonacea

Family Coelogorgiidae

2. *Coelogorgia palmosa* (Milne Edwards et Haime)(Aldabra, depth 9m)

Family Tubiporidae

3. *Tubipora musica* Linn   (C  etivy, D'Arros, Desroches, depth 10-34m)

Family Alcyoniidae

4. *Alcyonium flaccidum* Tixier-Durivault (Aldabra, depth 8m)
5. *Cladiella australis* (Macfadyen)(Mah  , depth 16m)
6. *Cladiella krempfi* (Hickson)(C  etivy, depth 8m)
7. *Cladiella sphaerophora* (Ehrenberg)(Praslin, depth 7m)
8. *Cladiella* sp. (C  etivy, Aldabra, Praslin, depth 5-8m)
9. *Dampia pocilloporaeformis* Alderslade (Bird, depth 12m)
10. *Lobophytum altum* Tixier-Durivault (C  etivy, depth 5-10m)
11. *Lobophytum borbonicum* Marenzeller (D'Arros, Desroches, La Digue, Farquhar, depth 8-12m)
12. *Lobophytum crebriplicatum* Marenzeller (African, depth 14m)
13. *Lobophytum irregulare* Tixier-Durivault (C  etivy, Desroches, depth 13-16m)
14. *Lobophytum michaelae* Tixier-Durivault (Farquhar, depth 15m)
15. *Lobophytum mirabile* Tixier-Durivault (Desroches, depth 12m)
16. *Lobophytum patulum* Tixier-Durivault (C  etivy, Desroches, La Digue, Cosmoledo, depth 5-14)

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17. *Lobophytum variatum* Tixier-Durivault (Farquhar, depth 16m)
18. *Lobophytum* sp. (Mahé, depth 4m)
19. *Parerythropodium fulvum* (Forskål)(Cœtivy, Aldabra, D'Arros, Mahé, Farquhar, St. Joseph, depth 6-24m)
20. *Sarcophyton ehrenbergi* Marenzeller (Cœtivy, D'Arros, Aldabra, Mahé, depth 3-16m)
21. *Sarcophyton elegans* Moser (D'Arros, depth 26m)
22. *Sarcophyton glaucum* (Quoy et Gaimard)(D'Arros, Desroches, Farquhar, depth 11-27m)
23. *Sarcophyton infundibuliforme* Tixier-Durivault (Cœtivy, African, Mahé, depth 6-15m)
24. *Sarcophyton roseum* Pratt (Cœtivy, depth 7m)
25. *Sarcophyton trocheliophorum* Marenzeller (Cœtivy, Desroches, Mahé, La Digue, Farquhar, depth 12-21m)
26. *Sarcophyton turschi* Verseveldt (Praslin, depth 8m)
27. *Sinularia cruciata* Tixier-Durivault (Cœtivy, depth 22m)
28. *Sinularia densa* (Whitelegge)(Cœtivy, depth 8m)
29. *Sinularia dura* (Pratt)(Cœtivy, depth 16m)
30. *Sinularia fishelsoni* Verseveldt (Cœtivy, D'Arros, Desroches, La Digue, Farquhar, depth 8-15m)
31. *Sinularia gibberosa* Tixier-Durivault (Cœtivy, D'Arros, Mahé, La Digue, depth 4-16m)
32. *Sinularia heterospiculata* Verseveldt (Cœtivy, Aldabra, Desroches, Farquhar, depth 13-17m)
33. *Sinularia humesi* Verseveldt (Farquhar, depth 15m)
34. *Sinularia leptoclados* (Ehrenberg)(Mahé, depth 14m)
35. *Sinularia lochmodes* Kolonko (Mahé, Bird, depth 12-14m)
36. *Sinularia mayi* Lütschwager (Cœtivy, Farquhar, African, depth 6-12m)
37. *Sinularia muralis* May (Desroches, depth 12m)
38. *Sinularia numerosa* Tixier-Durivault (Cœtivy, Desroches, Farquhar, depth 10-17)
39. *Sinularia polydactyla* (Ehrenberg)(Cœtivy, D'Arros, Desroches, Farquhar, Cosmoledo, depth 12-26m)
40. *Sinularia querciformis* (Pratt)(Mahé, depth 16m)
41. *Sinularia* aff. *robusta* Macfadyen (Cœtivy, depth 16m)
42. *Sinularia terspilli* Verseveldt (Mahé, depth 10m)
43. *Sinularia* sp. (Cœtivy, Farquhar, Cosmoledo, depth 12-15m)
- Family Nephtheidae
44. *Capnella bouilloni* Verseveldt (D'Arros, Desroches, African, St. Joseph, depth 5-25m)
45. *Capnella parva* Light (Cœtivy, D'Arros, Desroches, depth 8-24m)
46. *Lemnalia bournei* Roxas (Cœtivy, African, depth 5-14)
47. *Lemnalia tenuis* Verseveldt (Cœtivy, Aldabra, African, depth 16-32m)
48. *Litophyton arboreum* Forskål (Farquhar, depth 25m)
49. *Nephthea chabrolii* Audouin (Cœtivy, depth 10m)
50. *Nephthea hirsuta* Tixier-Durivault (Desroches, depth 13m)
51. *Spongodes mucronata* Pütter (Desroches, Praslin, Cosmoledo, depth 14-32m)
52. *Spongodes* sp.1 (Desroches, Cosmoledo, depth 24-33m)
53. *Spongodes* sp.2 (Cosmoledo, depth 31m)
54. *Stereonephthya acaulis* Verseveldt (Cœtivy, Aldabra, Desroches, Cosmoledo, depth 8-25m)
- Family Nidaliidae
55. *Siphonogorgia hicksoni* Thomson et Mackinnon (Desroches, depth 28m)
56. *Siphonogorgia* sp. (Desroches, depth 31m)
- Family Xenidiidae
57. *Anthelia glauca* Lamarck (Cœtivy, Aldabra, Farquhar, depth 3-6m)
58. *Cespitularia coerulea* May (Cœtivy, Farquhar, depth 4-16m)
59. *Heteroxenia elizabethae* Kolliker (Cœtivy, depth 4m)
60. *Sympodium caeruleum* Ehrenberg (D'Arros, Desroches, depth 8-12m)
61. *Xenia umbellata* Savigny (Mahé, depth 4m)
62. *Xenia* sp. (Cœtivy, Desroches, Mahé, depth 3-11m)

Order Gorgonacea

Family Subergorgiidae

63. *Subergorgia koellikeri* Wright et Studer (Praslin, African, depth 30-34m)

64. *Subergorgia mollis* (Nutting)(D'Arros, depth 22m)

65. *Subergorgia* sp. (D'Arros, Desroches, depth 18-30m)

Family Melithaeidae

66. *Melithaea ochracea* (Linné), Praslin, Farquhar, depth 14-33m)

67. *Wrightella coccinea* (Ellis et Solander)(Cœtivy, depth 8m)

Family Acanthogorgiidae

68. *Acanthogorgia* sp. (Desroches, depth 31m)

Family Plexauridae

69. *Euplexaura* aff. *erecta* Kükenthal (D'Arros, depth 28m)

70. *Paracis* sp. (Cœtivy, Praslin, Cosmoledo, depth 12-20m)

Family Gorgoniidae

71. *Rumphella aggregata* (Nutting)(Cœtivy, Desroches, Farquhar, Cosmoledo, depth 12-15m)

DISTRIBUTIONAL OBSERVATIONS

Stoddart (1984) distinguishes three main types of reefs in the Seychelles region, namely fringing reefs (Mahé, Praslin and other granitic islands), platform reefs (Cœtivy, Providence, African Banks, D'Arros and Desroches) and atoll reefs (Aldabra, Cosmoledo, Farquhar and St. Joseph). There are differences in the vertical distribution of octocorals on these reef types.

Fringing reefs. Octocorals on the reefs of this type are concentrated in the lower horizons of the reef slopes and sloping platforms. Colonies are situated well away from each other, therefore the alcyonacean living cover is not very high and does not exceed 25%. Usually 2-3 species dominate on these slopes. On the upper reef slope and reef-flat, alcyonaceans are uncommon. Only several species were found in these zones (*Sarcophyton ehrenbergi*, *Lobophytum* sp. and some xeniids). It is interesting that the domination by certain representatives of the family *Alcyoniidae* is noted for all the reefs studied in the Seychelles and also for other localities in the Indian Ocean, for example, Madagascar and Mozambique (personal observations). I have noted the same situation on most reefs of the South China Sea. Alcyoniids also contribute the main part of the reef octocoral fauna in Vietnam, moreover 84-92% of species belong to only four genera, namely *Sinularia*, *Sarcophyton*, *Lobophytum* and *Cladiella* (Malyutin, in press). A similar situation was noted in Thailand (Alderslade, personal communication), but on the Great Barrier of Australia, Dinesen (1983) noted the predominance of *Xeniidae* and *Nephtheidae*.

Platform reefs. One of the prominent features of these reefs is the absence of steep reef slopes with the reef surfaces inclining only slightly toward the open sea. Alcyonaceans are the most noticeable component of coral communities at depths of 4-6m and greater. Their vertical distribution is uniform and living cover averages 48%, but sometimes it may reach as much as 85% (Desroches Island), where the reef appears to be a peculiar "soft-coral platform." By comparison, the living cover of scleractinian and milleporid corals does not exceed 20%. Platform reefs are consistently dominated by representatives of the same genera, namely *Sinularia* (*S. polydactyla*, *S. heterospiculata*, *S. numerosa*, *S. fishelsoni* and several others), *Sarcophyton* (*S. trocheliophorum*, *S. ehrenbergi*), *Lobophytum* (*L. borbonicum*, *L. patulum*) and settlements are polyspecific. Representatives of other genera are uncommon here and settle singly or in small groups (*Capnella parva*).

Similar reefs were studied in Vietnam. The scheme of vertical distribution of octocorals on these reefs corresponds to those described above, and average living cover is approximately 70% for

similar "soft-coral platforms."

Atolls. With respect to octocoral distribution, atolls can be thought of as formations having the combined characters of both fringing and platform reefs. Variations in the distribution seem to be dependent upon the geomorphological peculiarities of each atoll. For example, the vertical distribution of octocorals on the eastern side of Farquhar is similar to that of platform reefs. The height and living cover of alcyonaceans (53% on average) and polyspecific settlement are evidence of this similarity. A definite reef slope is absent. An analogous situation occurs on the eastern rise of Cosmoledo, but the alcyonacean living cover is less (34% on average).

In contrast, the scheme of octocoral vertical distribution in some other atolls such as the north-western side of Farquhar, the western area of Aldabra and on some localities of St. Joseph correspond more closely with the characteristics of fringing reefs. Presence of a definite reef slope leads to concentrations of octocorals in the lower reef horizons. The average living cover of alcyonaceans near the base of the reef slope is about 30%, and values on the upper reef slope usually do not exceed 15%.

CONCLUSIONS

It appears that the vertical distribution of octocorals is influenced by the geomorphological peculiarities of each reef type. If a definite reef slope exists, octocorals are concentrated on the lower horizons of the reef. This is probably due to the tendency of dissolved and suspended organic matter and minerals to be directed down along the reef profile (Preobrazhensky, 1986). Octocorals tend to settle in these zones of organic matter transport and accumulation. In cases when there is a lack of definite reef slope, nutrients are distributed more uniformly along the reef profile and this presumably results in a uniformity of octocoral distribution.

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**CHAPTER 4
SPECIES COMPOSITION AND ABUNDANCE OF CORALS
AND OTHER INVERTEBRATES ON THE REEFS
OF THE SEYCHELLES ISLANDS**

BY

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CHAPTER 4
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BY

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INTRODUCTION

Coral reefs of the Seychelles Islands are not as well studied as those of Kenya, Madagascar and the Chagos Archipelago. Present knowledge is based on the collections of J. Stanley Gardiner made at the beginning of this century and on several later investigations performed on the reefs of Mahé Island and Aldabra Atoll (Gardiner 1936, Levi 1961, Lewis 1968, Rosen 1971, 1979). This study deals with the distributional patterns of corals, molluscs, sponges and other common macrobenthic invertebrates of the Seychelles Islands coastal zones.

METHODS AND MATERIALS

The investigation of species composition and distributions of macroinvertebrates was conducted from the R/V Akademik A. Nesmeyanov (January - March 1989) down to a depth of 30 m using a combination of frame-quadrats and transects (Maragos and Jokiel 1976, Bouchon 1981) depending on the extent and morphology of a given reef. When a reef extended for hundreds of meters offshore (e.g., Desroches, Farquhar, St. Joseph and Cerf Islands), the distribution of organisms was analyzed at a number of widespread stations 200-500 m from each other. In the coastal zones of the granitic islands (Mahé, Praslin, La Digue) and also on Cœtivy Island, a 100 m-transect marked at each meter was used. The animal populations and cover of corals were estimated using a 1.0 m² frame divided into 100 equal squares. At most sites, subtidal stations continued on seaward from intertidal transects.

Altogether, 33 profile sections (transects) in 13 localities were studied and the species composition of corals was determined for an additional 5 localities (Table 1), while the species composition of sponges was determined for 12 sites (Table 2). Representative collections were archived at the USSR Academy of Sciences, Far East Branch, Vladivostok.

RESULTS AND DISCUSSION

An analysis of the species composition and distributional patterns of the floristic and faunistic populations of reefs of the Seychelles showed that major upper subtidal communities in all areas

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studied are dominated by either scleractinian and alcyonarian corals, algae or seagrasses (for more detailed information on the flora of coastal waters of the Seychelles see Ch. 5, Gutnik et al., on alcyonarians - Ch. 3, Malyutin, of the present ARB issue). Abundances and the ratio of floristic and faunistic complexes substantially change from one island to another and even within one island area. This paper follows the descriptive scheme of reef classification for the Seychelles suggested by Stoddart (1984), who follows convention by dividing the reefs into three groups: fringing, platform and atoll reefs.

Fringing reefs were most typically found on Mahé Island. Near the northeast Point, at a distance of 120-130 m offshore, beds of the seagrass *Thalassodendron ciliatum* are replaced by a badly damaged reef built mainly by colonies of branched *Stylophora pistillata*, *Pocillopora verrucosa* and rarely by smaller colonies of massive *Porites*, which combined develop up to 3% cover of the calcareous or bedrock primary substrata. Considerable area here is covered with members of the order Corallimorpharia (subclass Hexacorallia). At a distance of 160-170 m offshore, the reef flat changes in slope inclining at about 25-30° down to 8-12 m in depth. Concomitantly, Scleractinia decrease in number and development (substratum area coverage no more than 1-2%); separate corallagenous blocks and landslips occur frequently. The gastropods *Cypraea histrio*, *Conus distans*, *Lambis chiragra*, the sea urchin *Diadema* as well as single individuals of the bivalve molluscs *Tridacna maxima* and *Pinctada margaritifera* can be found between scattered blocks. Farther seaward the sandy bottom is populated by massive, columnar and lamellar corals form at 12-15 m in depth. *Goniastrea*, *Favia*, *Favites*, *Galaxea*, *Montipora* and sponges of the genus *Spirastrella* are characteristic of this part of the reef. Single colonies of branched *Acropora*, which otherwise are well developed on reef slopes, are rare. Overall, coral cover reaches 80%. Similar compositions and vertical distributions of scleractinians were found near Anonim Island on the eastern coast of Mahé Island; however the coral cover on the reef slope is about 40%, and *Acropora*, *Pocillopora* and *Millepora* are more abundant here.

Granitic islands (Praslin, La Digue, Mahé) have fringing reefs in their coastal zones, which are characterized by a well developed reef flat and rather steep slopes extending down to 13-23 m in depth. The shallowest portions of reef flats and reef fronts are dominated by calcareous algae and encrusting scleractinians which are replaced by *Acropora* and *Pocillopora* (covering about 20-40%) at 2-3 m in depth. *Goniastrea* and *Favites* are common on large boulders and rocks. At 12 m in depth, the reef slope forms a platform inhabited by massive *Porites*, *Favia* and foliaceous *Pachyseris* (covering up to 30%). Among the other invertebrates, the gastropods *Lambis truncata* (1 individual·m⁻²), *Chicoreus ramosus* (1·m⁻²), *Lambis crocata* and smaller species are common.

At a distance of 2-3 km from Praslin Island, at 20-30 m in depth, the reef platform is populated by colonies of branched *Acropora* and *Turbinaria* as well as solitary *Heteropsammia cochlea*. At La Digue Island, coastal zone rock promontories 400-500 m offshore support isolated colonies of scleractinians, chiefly of the genera *Pocillopora* and *Favia*. In addition to corals, large settlements of the bivalve *Lopha cristagalli* (about 30·m⁻²) and *Pinctada margaritifera* (up to 20·m⁻²) are found.

According to Stoddart's (1984) classification, reefs of the African Banks, as well as reefs of Coëtivy, D'Arros, Cerf and Desroches, are indicative of platform reefs. Characteristic features of such reefs are a very slow increase in depth with increasing distance off shore, a long reef slope stretching over hundreds or even thousands meters, and extremely homogeneous compositions and distributions of organisms. The most salient features are given below, without describing each island in detail.

Reefs of Cerf Island and African Banks extend over several kilometers offshore and are 40-60% covered by 40-90% the seagrass *Thalassodendron ciliatum*. Of the scleractinians, branched *Stylophora pistillata*, *Porites cylindrica*, massive *Porites lutea* and *Favia* spp. are of most frequent

occurrence. There is no distinct zonation in the vertical distributional patterns of scleractinians in contrast to the typical fringing reefs of Mahé, Praslin and La Digue Islands. Coral colonies are not large (*Porites lutea* - < 20-30 cm in diameter), and total cover does not exceed 20%. Associated fauna includes the sea star *Protoreaster lincki* (to $2\cdot\text{m}^{-2}$) and the bivalve mollusc *Pinctada margaritifera* (about $1\cdot\text{m}^{-2}$).

In contrast to the reefs of the African Banks and Cerf Islands, the reef of the southeastern coast of D'Arros Island is smaller, with a more pronounced reef slope and scleractinian zonal pattern. Zonal alternation of monospecific populations is an interesting feature of this reef, the upper parts of which as a whole are similar in composition and development to the reefs described above. For example, the blue octocoral *Heliopora coerulea* is responsible for 100% cover at 17-25 m in depth. At 25-27 m (350-400 m from the reef front), separate juveniles of *Acropora*, *Heliopora* and the hydrocoral *Millepora* (about 50% cover) are replaced by monospecific populations of *Millepora platyphylla*, whereas at 27-30 m almost 100% of the substratum is occupied by *Acropora*. *Porites* and *Favia* become more common at greater depths where sand plains occur. On the reef as a whole, the gastropods *Lambis truncata*, *Lambis arhritica*, *Bursa bubo* and the holothurian *Telenota ananasare* are of frequent occurrence, but they do not form large concentrations.

The pattern of coral distribution in the coastal waters of Cœtivy Island represents an obvious case of local variability in vertical scleractinian distribution for the upper subtidal of the Seychelles. Abundant growths of the seagrass *Thalassodendron ciliatum* (90-100% cover) begin from the waterline along the northeastern coast of this island, and extend throughout the reef flat and gentle slope over 800-1000 m. With increased distance off shore, the abundance of *T. ciliatum* gradually decreases (about 50% at 7 m in depth and about 10% at 17 m in depth) whereas scleractinians and alcyonarians increase somewhat. At a distance of 400-500 m, coral cover reaches 30-35%, consisting of small colonies of branched *Acropora digitifera*, *Pocillopora verrucosa*, *Stylophora pistillata*, *Millepora platyphylla*, representatives of *Platygyra*, *Galaxea*, *Favia* and several smaller species usually inhabiting sites that are free of seagrasses, but sometimes co-occurring with these macrophytes.

Along the western coast of Cœtivy Island, *Thalassodendron ciliatum* occurs as a small belt between the coastline and the 1 m isobath. Immediately past the reef front, the scleractinian community begins with the dominant *Stylophora pistillata* densely covered with calcareous algae and *Acropora digitifera* (covering - 10-20%). Corals inhabit calcareous substrata together with the bivalves *Tridacna crocea* ($1\cdot\text{m}^{-2}$) and *Cardina variegata* (to $15\cdot\text{m}^{-2}$). At 10-12 m in depth, the coral cover consists of mainly *Heliopora coerulea* and *Acropora digitifera*, similar to the rock promontories of Praslin and La Digue Islands. Deeper, patches of *Acropora* and some colonies of *Porites* can be found.

The third group of Seychelles reefs consists of the atolls Aldabra, Astove, Farquhar, Cosmoledo and St. Joseph. As a rule, atolls are characterized by platform reefs on the outer side and surround a shallow sandy lagoon. Considerable areas of the lagoons are often occupied by seagrasses, spreading into intertidal sites. Scleractinians are sparse here, with only small isolated colonies of *Stylophora*, *Favia* and *Montipora*. Cover does not exceed 5% in most areas. The associated fauna is represented by the gastropods *Monetaria moneta*, *Monetaria annulus* (to $50\cdot\text{m}^{-2}$), *Cyprea tigris* ($0.2\cdot\text{m}^{-2}$), and by the bivalves *Pinna* sp. and *Codakia* sp.

The outer reef slopes facing the open sea, are often very extensive. Near the southeastern coast of St. Joseph Island, at distance of 1 km from shore (depth of about 25 m) a well-developed coral community is present with many scleractinians such as *Pocillopora*, *Porites* and *Acropora* (covering about 35%). *Favia*, *Favites*, *Lobophyllia*, *Symphyllia* and gorgonians are of frequent occurrence. A similar situation is observed in the coastal waters of Farquhar and Cosmoledo Islands. Also, the reef slope at the eastern end of St. Joseph Atoll has an inclination of 45-70° (30-40 m from the shore and

at 7 m in depth) and consists of the blue octocoral *Heliopora coerulea* at its upper boundary (100% cover), and of massive and encrusting scleractinian species (*Porites*, *Pachyseris*) below 24 m where *Heliopora* cover is reduced to 20-40%. At 33 m, the reef changes to a sandy platform with isolated small colonies of *Porites cylindrica* and some other species.

A slope of similar geomorphology is characteristic of the reef at the southwestern coast of Astove Atoll, where the reef at 6-8 m in depth is dominated by a monospecific cover of *Porites cylindrica* (100%) until it declines abruptly (inclination angle of 50-90°) down to more than 40 m. Beginning from 17-18 m, coral cover decreases sharply and *Porites cylindrica* is replaced by small colonies of *Platygyra* and *Favia*. Deeper than 22 m, corals are not observed in this region and the reef slope is nearly 100% covered by algae.

In summary, the Seychelles reefs, especially those of the northern granitic islands (Mahé, Praslin, La Digue), show scleractinian compositions and distributional patterns that are very similar to most reefs of the Indo-West Pacific (for observations in Vietnam see Latypov, 1987). More or less distinct vertical zonal patterns are similar, dependent on succession of scleractinians from the same genera and life forms (e.g., branched and crustose *Stylophora* and *Montipora* on reef flats, branched *Stylophora*, *Pocillopora* and *Acropora* on reef slopes and massive, encrusting and isolated *Porites*, *Pachyseris* and *Fungia* at the bases of slopes and on platforms). The preliminary checklist of Scleractinia and *Millepora* corals of the Seychelles includes 51 genera. Earlier surveys of Aldabra and other granitic islands identified a total of 64 genera of hermatypic corals (Rosen 1971, 1979, Pillai et al. 1973, Wijsman-Best et al. 1980, Sheppard 1987). Further study of the voucher collections will reduce this difference.

In conclusion, it is important to note the absence of dense settlements of bivalve molluscs on Seychelles reefs. Bivalves play an important role in the function of coastal benthic communities of the tropical zones of other Indian and Pacific Ocean reefs. For example, *Tridacna crocea*, on reefs in the region of Townsville (Australia), forms populations with a density of up to 200·m⁻² and is to a considerable degree responsible for the formation of micro atoll-like structures (Hamner and Jones 1976). In the coastal waters of Vietnam, this species along with other numerous and common Indo-Pacific molluscs, such as *Arca ventricosa* and *Begonia semiorbiculata*, seems to control important processes of bioerosion and biosedimentation. Only isolated individuals of these two species are also found on the Seychelles reefs. Bivalve molluscs are not as important for reef life in the Seychelles Islands as is the case on the Great Barrier Reef and in coastal zones of Vietnam, although their species diversity is comparatively high (Taylor 1968). The reasons for the differences in abundances of this invertebrate group in these regions is at present unclear.

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Table 1. Coral species from the coastal waters of the Seychelles Islands. M = Mahé, P = Praslin, Co = Cœtivy, F = Farquhar and D = Desroches

Species	Island				
	M	P	Co	F	D
1. <i>Pocillopora damicornis</i> (Linneus, 1758)	M	P			D
2. <i>Pocillopora eydouxi</i> Milne Edwards & Haime, 1860		P	Co		D
3. <i>Pocillopora meandrina</i> Dana, 1846					D
4. <i>Pocillopora verrucosa</i> (Ellis & Solander, 1786)	M	P	Co	F	D
5. <i>Pocillopora woodjonesi</i> Vaughan, 1918				F	
6. <i>Seriatopora hystrix</i> Dana, 1846			Co		D
7. <i>Stylophora pistillata</i> Esper, 1797	M	P	Co	F	D
8. <i>Montipora foveolata</i> (Dana, 1846)					D
9. <i>Montipora millepora</i> Crossland, 1952		P			
10. <i>Montipora spongodes</i> Bernard, 1897	M	P			
11. <i>Montipora venosa</i> (Ehrenberg, 1834)		P			
12. <i>Montipora verrucosa</i> (Lamarck, 1816)				F	
13. <i>Montipora</i> sp.1	M		Co	F	D
14. <i>Montipora</i> sp.2	M		Co	F	
15. <i>Anacropora</i> sp.		P			
16. <i>Acropora aculeus</i> (Dana, 1846)		P			
17. <i>Acropora anthocercis</i> (Brook, 1893)					D
18. <i>Acropora cerealis</i> (Dana, 1846)					D
19. <i>Acropora cytherea</i> (Dana, 1846)	M	P	Co		D
20. <i>Acropora digitifera</i> (Dana, 1846)	M	P	Co	F	
21. <i>Acropora divaricata</i> (Dana, 1846)	M	P		F	
22. <i>Acropora formosa</i> (Dana, 1846)	M	P			D
23. <i>Acropora grandis</i> (Brook, 1892)		P			D
24. <i>Acropora hyacinthus</i> (Dana, 1846)	M	P			D
25. <i>Acropora nasuta</i> (Dana, 1846)				F	D
26. <i>Acropora nobilis</i> (Dana, 1846)	M	P			
27. <i>Acropora palifera</i> (Lamarck, 1816)	M	P	Co		
28. <i>Acropora polystoma</i> (Brook, 1891)	M			F	
29. <i>Acropora robusta</i> (Dana, 1846)			Co		
30. <i>Acropora verweyi</i> Veron & Wallace, 1984			Co		
31. <i>Acropora</i> sp.1	M		Co	F	D
32. <i>Acropora</i> sp.2			Co		
33. <i>Astreopora explanata</i> Veron, 1985		P		F	
34. <i>Astreopora listeri</i> Bernard, 1896				F	
35. <i>Astreopora myriophthalma</i> (Lamarck, 1816)			Co		D
36. <i>Astreopora ocellata</i> Bernard, 1896		P			
37. <i>Astreopora</i> sp.				F	
38. <i>Porites annae</i> Crossland, 1952		P			
39. <i>Porites cylindrica</i> Dana, 1846			Co	F	
40. <i>Porites lobata</i> Dana, 1846	M	P	Co	F	D
41. <i>Porites lutea</i> Edwards & Haime, 1860	M			F	D
42. <i>Porites murrayensis</i> Vaughan, 1918					D
43. <i>Porites nigrescens</i> Dana, 1846					D
44. <i>Porites stephensoni</i> Crossland, 1952					D
45. <i>Porites</i> sp.				F	

Table 1. Continued.

Species	M	Island P	Co	F	D
46. <i>Goniopora lobata</i> Milne Edwards & Haime, 1860	M				D
47. <i>Goniopora</i> sp.1	M				
48. <i>Goniopora</i> sp.2	M				
49. <i>Alveopora</i> sp.	M				
50. <i>Pseudosiderastrea tayamai</i> Yabe & Sugiyama, 1935		P			
51. <i>Psammocora profundacella</i> Gardiner, 1898					D
52. <i>Psammocora superficialis</i> Gardiner, 1898					D
53. <i>Cosinaraea</i> sp.		P			
54. <i>Pavona clavus</i> (Dana, 1846)	M	P			D
55. <i>Pavona minuta</i> Wells, 1956	M	P		F	
56. <i>Pavona varians</i> Verrill, 1864		P			D
57. <i>Pavona</i> sp.				F	
58. <i>Leptoseris mycetoseroides</i> Wells, 1954				F	D
59. <i>Gardineroseris planulata</i> (Dana, 1846)		P		F	D
60. <i>Pachyseris</i> sp.	M	P			
61. <i>Cycloseris cyclolites</i> (Lamarck, 1801)			P		
62. <i>Diaseris</i> sp.		P			
63. <i>Fungia danai</i> Milne Edwards & Haime, 1851	M			F	
64. <i>Fungia granulosa</i> Klunzinger, 1879		P			
65. <i>Fungia repanda</i> Dana, 1846					D
66. <i>Fungia scutaria</i> Lamarck, 1801				F	
67. <i>Herpolitha limax</i> Houttuyn, 1772	M				D
68. <i>Herpolitha weberi</i> Van Der Horst, 1921					D
69. <i>Herpolitha</i> sp.					D
70. <i>Sandalolitha robusta</i> Quelch, 1886					D
71. <i>Galaxea astreata</i> (Lamarck, 1816)	M	P		F	
72. <i>Echinophyllia aspera</i> (Ellis & Solander, 1786)				F	D
73. <i>Mycedium elephantotus</i> (Pallas, 1766)		P			
74. <i>Pectinia lactuca</i> (Pallas, 1766)	M			F	
75. <i>Acanthastrea bowerbanki</i> Edwards & Haime, 1851				F	D
76. <i>Acanthastrea echinata</i> (Dana, 1846)				F	
77. <i>Acanthastrea hillae</i> Wells, 1955				F	
78. <i>Acanthastrea</i> sp.1	M				
79. <i>Lobophyllia</i> sp.	M				D
80. <i>Symphyllia</i> aff. <i>valenciennesii</i>	M				D
81. <i>Hydrophora microconos</i> (Lamarck, 1816)		P	Co	F	D
82. <i>Caulastrea</i> sp.		P			
83. <i>Favia maritima</i> (Nemanzo, 1971)	M		Co		D
84. <i>Favia maxima</i> Veron, Pichon & Wijsman-Best, 1977	M	P	Co		
85. <i>Favia pallida</i> (Dana, 1846)					D
86. <i>Favia speciosa</i> (Dana, 1846)	M	P	Co	F	D
87. <i>Favia stelligera</i> (Dana, 1846)		P	Co	F	
88. <i>Favia</i> sp.				F	
89. <i>Favites abdita</i> (Ellis & Solander, 1786)		P	Co	F	D
90. <i>Favites chinensis</i> (Verrill, 1866)	M			F	

Table 1. Continued.

Species	M	Island P	Co	F	D
91. <i>Favites flexuosa</i> (Dana, 1846)	M	P	Co	F	D
92. <i>Favites</i> sp.			Co		
93. <i>Goniastrea aspera</i> Verrill, 1905		P			
94. <i>Goniastrea edwardsi</i> Chevalier, 1971	M	P			D
95. <i>Goniastrea pectinata</i> (Hemprich & Ehrenberg, 1834)	M	P	Co	F	D
96. <i>Goniastrea retiformis</i> (Lamarck, 1816)	M	P			D
97. <i>Platygyra daedalea</i> (Ellis & Solander, 1786)	M		Co	F	D
98. <i>Platygyra lamellina</i> (Hemprich & Ehrenberg, 1834)			Co	F	
99. <i>Platygyra pini</i> Chevalier, 1975	M			F	
100. <i>Platygyra sinensis</i> (Edwards & Haime, 1849)		P			
101. <i>Leptoria phrygia</i> (Ellis & Solander, 1786)			Co		
102. <i>Oulophyllia crispa</i> (Lamarck, 1816)	M			F	D
103. <i>Montastrea annuligera</i> (Edwards & Haime, 1849)		P		F	D
104. <i>Plesiastrea versipora</i> (Lamarck, 1816)			Co		D
105. <i>Diploastrea heliopora</i> (Lamarck, 1816)					D
106. <i>Leptastrea bewickensis</i> Veron, Pichon & Wijsman-Best, 1977					D
107. <i>Leptastrea purpurea</i> (Dana, 1846)	M	P			D
108. <i>Leptastrea transversa</i> Klunzinger, 1879	M				
109. <i>Cyphastrea serailia</i> (Forskål, 1775)		P	Co		
110. <i>Cyphastrea</i> sp.	M				
111. <i>Echinopora lamellosa</i> (Esper, 1795)	M				
112. <i>Moseleya latistellata</i> Quelch, 1884					D
113. <i>Turbinaria frondens</i> (Dana, 1846)	M	P	Co		D
114. <i>Turbinaria mesenterina</i> (Lamarck, 1816)	M	P			D
115. <i>Turbinaria peltata</i> (Esper, 1794)	M	P	Co		D
116. <i>Turbinaria reniformis</i> Bernard, 1896			Co		
117. <i>Heteropsammia cochlea</i> (Spengler, 1781)	M	P			
118. <i>Tubastraea micrantha</i> (Hemprich & Ehrenberg, 1834)					D
119. <i>Tubastraea</i> sp.	M				D
120. <i>Siderastrea radians</i> (Pallas, 1766)		P			
121. <i>Tubipora musica</i> Linnaeus, 1758			Co		D
122. <i>Heliopora coerulea</i> (Pallas, 1766)		P	Co	F	D
123. <i>Millepora platyphylla</i> Hemprich & Ehrenberg, 1834	M	P	Co	F	D



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**CHAPTER 5
SPECIES COMPOSITION, DISTRIBUTION AND ABUNDANCE
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SEYCHELLES ISLANDS**

BY

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CHAPTER 5
SPECIES COMPOSITION, DISTRIBUTION AND ABUNDANCE OF
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SEYCHELLES ISLANDS

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A.A. Kalugina-Gutnik^{*}, L.P. Perestenko^{**} and T.V. Titlyanova^{***}

INTRODUCTION

Marine algae and seagrasses of the Republic of the Seychelles remain poorly studied. Macrophytic algae reported for the area (about 120 species) were collected between 1899-1990 by J. Stanley Gardiner during the *Sealark* Expedition to the Indian Ocean (Gepp and Gepp 1909; 1911, Weber van Bosse 1913a, 1913b). Aleem (1984) reported 9 species of seagrasses and 22 algal species for the macrophyte communities of Mahé, Latam, Aldabra, Comoro, Farquhar and Amirantes Islands. Subsequently, 5 seagrasses and 33 algal species were recorded (Titlyanova and Butorin 1987) for Mahé and Coëtivy Islands, half of these representing new records. There are no data on either algae or seagrasses for 12 of the Seychelles island groups. The present study of these island groups focused on: (1) macrophytic species composition; (2) distribution of algae and seagrasses at different depths for typical ecotopes; and (3) the structure of benthic plant communities (phytocoenoses), including determination of biomass for macroalgae and seagrasses.

METHODS AND MATERIALS

Studies were conducted at Coëtivy Atoll, Desroches, African Banks, Providence, Farquhar Atoll, Aldabra Atoll, St. Joseph Atoll, Cosmoledo Atoll, Astove Atoll, Mahé, Praslin and La Digue Islands. Quantitative and qualitative samples were collected using transects and square quadrats from the upper intertidal zone to a depth of 30-50 m, using a combination of snorkle and SCUBA diving techniques. In each intertidal horizon, four 25 x 25 cm quadrats were selected and sampled in representative habitats with vegetation coverage averaging 10-15%. In the subtidal zone, one 50 x 50 cm quadrat was harvested at each station.

A total of 687 samples (479 quantitative harvest samples) were taken at 257 stations. Vegetation was described for 28 intertidal and 37 subtidal transects. About 4000 plant specimens were collected and duplicates are deposited in the herbaria of all three authors' institutions. Altogether, 327 algal species and 8 seagrass species were documented for the 12 island systems (Table 1).

Intertidal zones were surveyed during periods of low water at which time type of substratum, bottom relief, vegetation coverage and the width of vegetation belts were determined. Laboratory

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processing included determination of the population density (individuals·m⁻²), wet biomass (g·m⁻²), plant height and species composition. Macroalgae were identified using the following works: Børgesen (1914, 1915, 1916, 1917, 1918, 1919, 1920, 1940, 1941, 1942, 1943, 1944, 1945, 1946, 1948, 1949, 1950, 1951, 1952, 1953, 1954, 1957), Cordero (1977), Colinvaux (1968), Dawson (1954), Durairatham (1961), Egerod (1975), Hartog (1970), Hillis (1959, 1980), Kraft (1986), Misra (1966), Olsen-Stojkovich (1985), Pham-Hoang Ho (1967, 1969), Tanaka and Pham-Hoang Ho (1962), Taylor (1960) and Valet (1969).

The structure of phytocoenosis (community associations) was analyzed with the use of the Shannon species diversity index (Wilhm 1968),

$$H = \frac{W \lg_w - \sum_i W_i \lg W_i}{W \lg_2}$$

where: H - species diversity of a sample; W_i - biomass of the i-th species sampled (g·m⁻²); W - total biomass of the sample (g·m⁻²) and s - number of species in the sample. At H = 0 - 0.8 the phytocoenosis structure was considered to be monodominant; at H = 0.9 - 1.5 - oligodominant and at H > 1.5 - polydominant.

STUDY AREAS

The Seychelles islands surveyed can be divided into three groups by their structure and the type of bottom vegetation. The first group includes: Cœtivy, Desroches, African Banks and Providence; the second: Farquhar, Aldabra, St. Joseph and D'Arros, Cosmoledo and Astove; and the third: Mahé, Praslin and La Digue. Cœtivy, Desroches, African Banks and Providence are calcareous and fringed with barrier reefs. Farquhar, Aldabra, St. Joseph and D'Arros, Cosmoledo and Astove are atolls with shallow sand lagoons and sand banks exposed at low waters. On their ocean sides, these atolls are fringed with a broad (250-1000 m) reef-flat, pre-slope platform and reef slope. The intertidal zone of these islands is mostly wide (100-1000 m), sloping and uniform in structure. The upper and the middle horizons of the intertidal zone consist of sand. The lower horizon is sandy with pits, or built of dead consolidated corals covered with sand. The subtidal zone has different relief and substrata: the upper reef edge is sandy. The reef edge is built of coral plates and blocks above a steep sandy slope covered with dead corals with live coral colonies. The upper intertidal horizon is usually devoid of vegetation; a wide belt of seagrasses spreads from the middle horizon of the intertidal zone down to depths of 15-20 m. Greater depths are occupied by *Halimeda* communities. Cœtivy is the most thoroughly studied island in the first group.

Mahé, Praslin and La Digue, the third group, are high granitic islands with numerous inlets and are fringed by narrow reefs. Vegetation of the carbonate islands (groups 1 and 2) is dominated by seagrasses, and red and green algae. While on these granitic islands, brown algae (Phaeophyta), mostly *Sargassum*, predominate in plant communities along with seagrasses.

RESULTS AND DISCUSSION

Cœtivy Island

The benthic vegetation was surveyed along nearly the entire coastline (Fig. 1) and showed uneven distributional patterns. At the northern point of the island, the intertidal zone is narrow (5-10 m in width), sandy and devoid of vegetation. Macrophytic growth begins at a depth of 2-3 m, a

distance of 100-150 m from the shoreline. The southernmost intertidal zone is broad (500-1000 m in width) with numerous intertidal pools at low waters. Along the eastern and western coasts, the intertidal zone does not exceed 500 m in width. Settlements of *Enteromorpha kylinii* sometimes occur on individual coral blocks in the upper intertidal horizon. The middle horizon is occupied by the seagrasses *Syringodium isoetifolium*, *Halodule uninervis* and *Thalassodendron ciliatum* (Fig. 2, Table 2) characterizing the major associations (or phytocoenoses, characterized by dominant species). The species composition of these associations is limited, including among the dominant species, *Jania adhaerens*, *Hypnea pannosa*, *Dictyosphaeria setchellii*, *Boodlea composita* and *Halimeda gracilis*.

The lower intertidal horizon is dominated by *Thalassodendron ciliatum*. *Halimeda gracilis*, *H. stuposa*, *H. micronesica*, *Dictyurus purpurascens* and *Laurencia* sp. are subdominants in all associations dominated by *T. ciliatum*. Dense mats of *Gelidiella acerosa*, *Laurencia parvipapillata*, *L. paniculata* and *Halimeda opuntia* develop at the stem bases and on the rhizomes of *T. ciliatum*, while the stems are populated by the algal epiphytes *Haloplegma duperreyi*, *Gelidiella myrioclada*, *Champia parvula*, *Ceramium fastigiatum*, *Lophosiphonia villum*, *Polysiphonia* sp. and *Centroceras apiculatum*. Among the other organisms noted were *Dictyosphaeria cavernosa*, *D. setchellii*, *Caulerpa sertularioides*, *Udotea argentea*, *U. orientalis*, *Laurencia obtusa*, *Dictyurus purpurascens*, *Jania unguolata* and *Valonia aegagropila*. Scattered individuals of *Lobophora variegata* and *Turbinaria ornata* occur on the reef edge.

Twelve associations were distinguished in the intertidal zone (Table 2), ranging in structure from mono- to oligo-dominant (i.e., $H = 0 - 0.8$ and $0.9 - 1.6$, respectively) with well developed plant coverages ranging from 70-100%. In the sublittoral zone, associations of *Thalassodendron ciliatum* - *Halimeda* dominate the sandy reef slope among coral debris (Fig. 2). Biomass of these two dominant species contributes 80-100% to the association (Fig. 1), which includes almost all the species recorded for the lower intertidal horizon. In addition, *Rhipilia tomentosa*, *Heterosiphonia* sp., *Lophocladia trichoclados*, *Griffithsia subcylindrica*, *Chlorodesmis comosa*, *Kallymenia* sp., *Coelarthrum boergesenii*, *Tricleocarpa oblongata*, *Liagora divaricata* and *Botryocladia skottsbergii* were also found. The lower border of the association extends to a depth of 15-20 m with isolated specimens of *T. ciliatum* occurring to depths of 30-33 m. One of the most prominent species of subtidal coenoses is *Halimeda opuntia*. Off the southwestern border of the island, phytocoenoses of *Halimeda* appear at 1-m deep on the sand plateau and extend down to depths of 30-50 m and over vast areas. The biomass of *Halimeda* increases from 429 to 5078 g·m⁻² at depths between 1-5 m (Table 2; Fig. 1; Stations 15-20). Species composition of the phytocoenosis is limited, with the associated species being *T. ciliatum*, *Lobophora variegata*, *Caulerpa cupressoides*, *Haloplegma duperreyi*, *Dictyurus purpurascens* and *Heterosiphonia* sp.

At depths of 30-50 m, dominants were *Avrainvillea amadelpha* f. *submersa*, *Halimeda copiosa*, *Caulerpa* sp., *Dasya* sp., *Struvea elegans*, *Antithamnion* sp., *Chrysomenia pyriformis*, *Peyssonnelia* sp. and *Anadyomene wrightii*. The associations are characterized by a monodominant structure with sparse and low-statured vegetation coverage (Table 2). The H index of species diversity ranges mainly from 0 to 0.7, but in some phytocoenoses it exceeds 1.0 (Table 2).

The distributional pattern of common species of algae and seagrasses around Coetivy is shown in Figure 3. The lower intertidal horizon and the upper sublittoral horizon down to a depth of 7-10 m (Fig. 4) show the greatest biomass of macrophytes (mean of 3096 ± 393 S.D. g·m⁻²). Ranking second in biomass (1597 ± 272 g·m⁻²) are phytocoenoses at 10-20 m in depth along the eastern coast and in the lower intertidal zone of the southern end of the island. Closest to the shore, within the middle horizon of the intertidal zone, the mean biomass of macrophytes is 878 ± 306 g·m⁻². The lowest biomass (557 ± 157 g·m⁻²) was found at greater depths. The total area of algal and seagrass growths around Coetivy Island is approximately 13,190 ha, with an estimated total standing stock of

196,316 t wet weight. On average, 1 ha supports 15 t phytomass.

Altogether, 113 plant species were found at Coetivy, 4 of which are seagrasses. The 109 algal species include 58 Rhodophyta, 46 Chlorophyta, 4 Phaeophyta and 1 Cyanophyta (Table 1).

Desroches Island

The marine benthic vegetation of the island was studied in considerable detail (Figs. 5-7). The upper intertidal zone is similar to that of Coetivy Island. An association of *Thalassia hemprichii* with *Potolithon gardineri* forms in the middle horizon. The phytocoenosis is oligodominant in structure, vegetation coverage averages 80-100%. Population density and biomass do not exceed 1536 individuals·m⁻² and 2471 g·m⁻², respectively (Table 2). Among the associated species, *Udotea orientalis*, *Caulerpa cupressoides*, *C. serrulata*, *Dictyosphaeria cavernosa* and *Jania capillacea* are common. In the lower intertidal horizon, *Thalassodendron ciliatum* forms three associations (characterized by their dominant species): *Thalassodendron ciliatum* + *T. hemprichii* - *Halimeda micronesica*, *T. ciliatum* - *Halimeda opuntia* and *T. ciliatum* alone. Biomass of *T. ciliatum* accounts for 60-100% of the total biomass of the three phytocoenoses (Fig. 5). Population density and biomass are high, up to 2600 individuals·m⁻² and 5095 g·m⁻² (Table 2), respectively. The stalks of *Thalassodendron ciliatum* are densely overgrown with epiphytes. The most common associated species are *Laurencia parvipapillata*, *L. papillosa*, *Dasya mollis*, *Dictyurus purpurascens*, *Struvea anastomosans*, *Haloplegma duperreyi*, *Hypnea esperi*, *H. spinella*, *Gelidiella lubrica*, *G. myrioclada*, *Heterosiphonia crispella*, *Jania capillacea*, *J. unguolata*, *Dictyosphaeria cavernosa*, *D. vershyusii*, *Caulerpa serrulata*, *C. cupressoides*, *Valonia aegagropila*, *V. fastigiata* and *Halimeda stuposa*, with *Laurencia*, *Jania* and *Halimeda* forming mats.

In terms of depth of habitat, community structure, species composition and the main quantitative characteristics, subtidal associations of *Thalassodendron ciliatum*-*Halimeda* at Desroches Island do not differ appreciably from corresponding associations at Coetivy Island (Table 2). In addition to species that were also common on Coetivy Island, we found *Neomeris bilimbata*, *Caulerpa mexicana*, *Halymenia* sp., *Liagora pennata*, *Galaxaura marginata*, *Tricleocarpa oblongata*, *G. rudis*, *Haliptilon subulatum* and *Lomentaria mauritiana*. In the depth range between 15-20 and 35-38 m, a steep cliff partly fringing the island is covered with sparse algal growths. Below the cliff, a *Halimeda* phytocoenosis extends to a depth of 50 m (Table 2), with high species diversity of associated algae, most of them being common in the upper subtidal and lower intertidal zones. Typical of these deep waters were *Avrainvillea amadelpha* f. *submersa*, *Halimeda copiosa*, *H. tuna*, *Dudresnaya* sp., *Caloglossa* sp., *Hypoglossum* sp. and *Caulerpa mexicana*. Altogether, 132 plant species, including 3 seagrasses and 129 algal species (72 red algae, 50 green algae, 5 brown algae and 2 blue-green algae) were collected near Desroches Island. In general, the bottom vegetation of Desroches Island is characterized by relatively high quantitative indices (Fig. 8). The total area covered by benthic vegetation is about 711 ha and supports about 16,581 t wet plant biomass.

African Banks

The South Island's lower intertidal and upper subtidal zones (Figs. 9-11) are characterized by associations of *Thalassia hemprichii* + *Thalassodendron ciliatum* - *Microdictyon montagnei*. *Thalassodendron ciliatum* is responsible for 40-100% of the total biomass of all phytocoenoses (Fig. 9). In the subtidal zone, this association is replaced by the *T. ciliatum* association which extends along the slope of the reef down to a depth of 20-25 m. The population density and biomass in the *T. ciliatum* association is significantly lower than on Coetivy and Desroches Islands (Table 2). Common associated species were *Halimeda micronesica*, *H. stuposa*, *H. gracilis*, *H. macroloba*, *H. opuntia*,

Dictyosphaeria cavernosa, *D. verluysii*, *Rhipilia tomentosa*, *Anadyomene plicata*, *Struvea anastomosans*, *Tricleocarpa oblongata*, *Haloplegma duperreyi* and *Lobophora variegata*. The deep-water association of *Halimeda* sp. (25-37 m) is characterized by a rich species diversity of associated algae similar to that near Desroches Island. Most characteristic were *Halimeda stuposa*, *H. micronesica*, *Caulerpa cupressoides*, *Avrainvillea amadelpha* f. *submersa* and *Udotea orientalis*. Several species were found only at the 37 m depth (Station 200): *Halophila stipulacea*, *Caulerpa* sp., *Boergesenia forbesii*, *Boodleopsis pusilla*, *Anotrichium tenuis*, *Galaxaura rudis* and *Chrysomenia pyriformis*. *Tydemania gardineri*, *Halophila stipulacea* and *Anadyomene plicata* were found only near South Island. Altogether, 84 plant species were collected near South Island: 3 seagrasses and 81 algae (47 red algae, 31 green algae, 3 brown algae and 3 blue-green algae).

Providence Atoll

The intertidal zone of the southern coast of Cerf Island (Fig. 12, 13) is sandy, almost devoid of vegetation, with scattered coral debris covered by *Enteromorpha clathrata*. The distribution of plant communities in the subtidal zone was typical of the other islands of this group. At a depth of 20-23 m, the *Thalassodendron ciliatum* association is replaced by communities dominated by *Halimeda gracilis* extending the down to 32 m (Table 2). *Thalassodendron ciliatum* associates include *Microdictyon montagnei*, *Herposiphonia secunda* f. *tenella*, *Dictyurus purpurascens*, *Griffithsia subcylindrica* and *Cottoniella arcuata*. The *Halimeda* communities included *Halimeda micronesica*, *Microdictyon montagnei*, *Valonia fastigiata*, *Caulerpa brachypus*, *Tricleocarpa oblongata*, *Galaxaura rudis* and other minor species. Two seagrass species and 58 algal species (40 red algae, 16 green algae and 2 brown algae) were collected near Cerf Island.

The intertidal vegetation of islands of the first and second groups is similar in structure and distribution. The upper, and sometimes mid-tidal horizons, are devoid of plant coverage. The middle and lower intertidal horizons support associations of *Thalassia hemprichii* + *Thalassodendron ciliatum*. In the lower intertidal and subtidal horizons, this association is replaced by communities of *T. ciliatum* and green algae, which become more frequent in all phytocoenoses compared with those of the islands of the first group.

Farquhar Atoll

At Farquhar Atoll, *Thalassia hemprichii* + *Thalassodendron ciliatum* associations of North Island, South Island, Bird Island and the lagoon (Figs. 14-17) had moderate population densities and biomasses (Fig. 15, Table 2). Plant coverage near South Island ranges from 5 to 40% and 100% near North Island. Macrophyte associations include *Boodlea struveoides*, *Valonia aegagropila*, *Cladophoropsis sundanensis*, *Dictyosphaeria cavernosa* and *D. verluysii*. The green algae *Cladophora socialis* and *B. struveoides* form monodominant intertidal phytocoenoses. *Boodlea struveoides*, *Caulerpa cupressoides* and *Valonia aegagropila* are included as subdominant species in both the *Thalassodendron ciliatum* - *B. struveoides* and *T. ciliatum* - *V. aegagropila* - *C. cupressoides* (Table 2) plant associations. The phytocoenoses also include *Microdictyon okamurai*, *Dictyosphaeria cavernosa*, *Cladophoropsis sundanensis*, *Jania adhaerens*, *J. unguolata*, *Gelidiella pannosa*, *G. myrioclada*, *G. lubrica*, *Lophosiphonia villum*, *Ceramium fastigiatum* and *Hypnea esperi*. *Haloplegma duperreyi*, *Liagora ceranoides*, *Laurencia papillosa*, *L. obtusa* and *Lobophora variegata* are epiphytic on the stems of *T. ciliatum* at the reef edge.

The subtidal zone vegetation is poorly developed on the reef slope, because abundant coral populations extend almost to the reef-front. The following phytocoenoses were distinguished at depths of 3-17 m: *Caulerpa cupressoides* + *Boodlea struveoides*, *Halimeda opuntia* + *C. cupressoides*

and *Thalassodendron ciliatum* - *Halimeda*. With increasing depth these were replaced by phytocoenoses of *M. okamurai* + *B. struveoides*, *Microdictyon* and *Udotea* + *Caulerpa* (Table 2). Plant coverage ranges from 5 to 90%, but more often 5-30%. The height of vegetative cover is not great (1-2, seldom more than 1 cm) and the biomass is small (261-520 g·m⁻²).

Species richness of algae in the subtidal zone is low, and does not change with depth. Such species as *M. okamurai*, *C. cupressoides*, *B. struveoides*, *H. opuntia* and *Struvea anastomosans*, are widespread at 35 m. The epiphytes *Haloplegma duperreyi*, *Jania unguolata*, *Gelidiella myrioclada*, *G. lubrica*, *Griffithsia subcylindrica*, *G. metcalfii*, *Heterosiphonia crispella* and *Lophocladia trichoclados* inhabit the stems of *T. ciliatum*. *Turbinaria ornata* and *Lobophora variegata* also occur but are rare.

Sargassum ilicifolium was found between 1-4 m deep on a sunken vessel at the southwestern end of the atoll representing the only low island location where the genus occurred. *Ulva rigida*, *Boodlea struveoides*, *Dictyosphaeria cavernosa*, *Struvea anastomosans*, *Cladophora laetevirens*, *Dictyopteris delicatula*, *Padina* sp., *Sphacelaria rigidula*, *Gelidium pusillum*, *Jania unguolata*, *Hypnea esperi* and *H. pannosa* occurred with the *Sargassum*.

The vegetation of the lagoon is considerably richer than that of the outer reef slope. It is characterized by the *Thalassodendron* - *Halimeda* phytocoenosis (Figs. 14-17; Table 2). The central part of the lagoon is covered with sand and corals and is devoid of vegetation. In the southern region of the lagoon, sites with *Thalassodendron ciliatum* phytocoenoses are rare. The belt of *Thalassia hemprichii* + *T. ciliatum*, including species of *Laurencia* and *Halimeda*, runs along the northwestern reef edge. Northern and western parts of the lagoon are occupied by dense populations of *T. ciliatum*, which is responsible for 60-95% of the plant biomass. *Halimeda opuntia*, *Caulerpa cupressoides* and *Microdictyon okamurai* are community subdominants. *Halimeda gracilis*, *Caulerpa serrulata*, *C. peltata*, *C. racemosa*, *C. mexicana*, *Valonia aegagropila*, *Boodlea struveoides*, *Laurencia obtusa*, *L. papillosa*, *Hypnea esperi*, *Jania unguolata*, *J. capillacea*, *Centroceras apiculatum*, *Ceramium fastigiatum* and *Gelidiella lubrica* are of frequent occurrence. At Farquhar Atoll, an estimated 195,139 t of benthic phytomass occupies an area of 10,085 ha. Altogether near Farquhar Atoll, 2 seagrasses and 115 algal species (including 66 red, 39 green, 7 brown and 3 blue-green species) were found.

Aldabra Atoll

The structure of the Aldabra Atoll differs considerably from some of the other island groups, since its coasts are built primarily of dead consolidated corals and are steeply undercut and overhang the water. Surveys were conducted mostly on the western coast of the atoll near Bua Passage in the lagoon and on the outer part of the reef, as well as the southeastern parts of the atoll (Figs. 18-20). A polydominant association of *Thalassodendron ciliatum* - *Thalassia hemprichii* - *Halimeda* forms in the lower intertidal horizon (Table 2). *Thalassodendron ciliatum* is responsible for 40-90% of the community biomass, while *T. hemprichii*, *Halimeda opuntia*, *Caulerpa cupressoides* and *Laurencia* combine to contribute 60-10%. In addition to the above species, the phytocoenosis includes *Laurencia*, *Hypnea* and *Jania* species forming dense mats. The stems of *T. ciliatum* are overgrown with epiphytes, including *Ulva rigida*, *Hypnea esperi*, *Dasya mollis*, *Dictyurus purpurascens*, *Heterosiphonia* sp., and occasionally *Lobophora variegata* and *Syringodium isoetifolium* are present. At the lower border of the intertidal zone, the association of *Thalassodendron* - *Thalassia* - *Halimeda* is replaced by a *T. ciliatum* association which forms a belt 400-500 m in width along the entire western coast. On the reef slope, *T. ciliatum* populations disappear at 10 m in depth on a sandy bottom with abundant dead coral debris. The most common associated species are *Ulva rigida*, *Halimeda opuntia*, *H. tuna*, *H. gracilis*, *H. micronesica*, *Lobophora variegata*, *Turbinaria ornata*, *Spyridia filamentosa*, *Acanthophora spicifera*, *Dasya mollis*, *Caloglossa adnata* and species of

Ceramium, *Hypnea* and *Gelidiella*. *Wurdemannia miniata*, *Gelidiella myrioclada* and *Ulva rigida* grow on the stems of *T. ciliatum*. Depths to 12-35 m are occupied by simple monodominant phytocoenoses of *Halimeda*. These phytocoenoses include a considerable number of species similar to that of the *T. ciliatum* association. Additionally, *Chlorodesmis comosa*, *Avrainvillea amadelpha* f. *submersa*, *Acetabularia parvula*, *A. clavata*, *Boergesenia forbesii* and *Chondria polyrhiza* occur here.

The lagoon is connected with the ocean by the Bua Passage (depth of 5-6 m). The passage bottom is swept by strong currents and is hard and sandy with settlements of black gorgonians. Often the dead coral debris is populated by extensive growths of *Thalassodendron ciliatum* (Station 93). *Thalassodendron* leaves and stems are devoid of epiphytes, probably because of the strong current in the passage. Seagrass growths spread into the lagoon and occupy a zone 600-800 m from the shore where the depth decreases sharply. On shallow intertidal areas of the lagoon, vegetative coverage is composed of numerous assemblages, the most common of which is a phytocoenosis dominated by *Spyridia filamentosa*. A phytocoenosis of *Thalassia* - *Halimeda* occupies the area near the coast along the northern part of the lagoon (Fig. 18; St. 90; Table 2). Opposite the passage, phytocoenoses of *Turbinaria* - *Halimeda* (St. 91) and *Thalassodendron* - *Laurencia* - *Halimeda* (St. 89) are present. Plant communities of the lagoon have oligo- to poly-dominant structures, mosaic patterns of the phytocoenoses and rich macrophyte compositions.

Near Aldabra Atoll, 4 seagrass species and 119 algal species (i.e., 73 Rhodophyta, 40 Chlorophyta, 4 Phaeophyta, and 2 Cyanophyta) were collected.

Cosmoledo Atoll

The bottom vegetation of the reef slope and lagoons was surveyed at depths from 4 to 42 m near Wizard and Pagoda islands (Figs. 21, 22). The vegetative coverage at 4-20 m depths is poorly developed and consists of separate groups with dominants consisting of species of *Laurencia*, *Turbinaria*, *Galaxaura*, *Caulerpa* and *Boodlea*. Below 20 m, *Halimeda*, *Microdictyon* and *Avrainvillea* species predominate (Table 2). *Thalassodendron ciliatum*, *Microdictyon* and *Avrainvillea* species predominate (Table 2). *Thalassodendron ciliatum* phytocoenoses, common in the majority of the atolls surveyed, were not found in the subtidal zone. Most of the species found at this coastal site occur at all depths examined and do not reveal any definite regularity in vertical distribution. The following species were found rarely or for the first time: *Neomeris vanbosseae*, *Caulerpa webbiana*, *C. sp.*, *Acetabularia pusilla*, *Mesophyllum mesomorphum*, *Hydrolithon breviclavium*, *Wrangelia argus*, *Ceramium huysmansii*, *Sphacelaria tribuloides* and *Phaeophila dendroides*.

The lagoon contains a rich vegetative cover. The vast sandy shallow water areas between the islands Wizard and Polit and the coastal zone of Wizard are occupied by an association dominated by *Halodule uninervis*. An association of *Thalassia* + *Cymodocea* is situated somewhat farther from the shore. An association dominated by *Thalassodendron ciliatum* - *Laurencia* was found between 0.4-5.5 m in depth. The central and western parts of the lagoon are occupied by an association of *T. ciliatum* - *Halimeda opuntia* (Table 2). The coenobionts *Laurencia papillosa*, *Caulerpa racemosa*, *C. cupressoides*, *C. sp.*, *Microdictyon okamurai* and *Chaetomorpha capillare* are typical members of the association.

The species composition of the lagoon algae is uniform and includes mostly green algae. In addition to the above mentioned species, *Boergesenia forbesii*, *Dictyosphaeria cavernosa*, *Neomeris annulata*, *Lobophora variegata* and *Haloplegma duperreyi* were found here. Cosmoledo Atoll contained 4 seagrass species and 106 algal species, including 60 red, 42 green and 6 brown algae.

St. Joseph Atoll

The southern coast of D'Arros and Resourse islands and the eastern, northeastern and southern coasts of St. Joseph Island were surveyed. The distribution of seagrass communities over the intertidal zone of D'Arros and St. Joseph islands is typical of the other systems (Figs. 23-25; Table 2). A phytocoenosis dominated by *Thalassodendron* - *Thalassia* is replaced by a phytocoenosis of *Cladophoropsis sundanensis* + *Valonia fastigiata* in the lower intertidal horizon near D'Arros island. The dominant species are all mat formers. *Boodlea struveoides*, *Dictyosphaeria verluyssii*, *Microdictyon montagnei*, *Jania capillacea* and *Gelidiella pannosa* also occur here. The reef edge is exposed to a heavy wave action and is devoid of vegetation. Separate populations of *Halimeda gracilis* and *Botryocladia skottsbergii* occur at depths of 3-5 m. Deeper substrata are covered by crustose algae, such as *Fosliella*, *Peyssonnelia* and *Neogoniolithon*, and by corals.

Resourse Island

Two communities dominated by *Thalassodendron* - *Microdictyon* or *Thalassodendron* form in the lower intertidal and upper subtidal zones of Resourse island. *Halimeda* communities occupy depths of 7-37 m (Table 2). *Thalassia hemprichii* dominates the areas exposed to air at low waters. In the lagoon of St. Joseph Island, *T. ciliatum* tends to predominate with increasing depth. *Microdictyon okamurai*, *M. montagnei*, *Boodlea struveoides*, *Dictyosphaeria cavernosa*, *D. verluyssii*, *Valonia fastigiata*, *Udotea orientalis*, *Halimeda stuposa*, *H. micronesica* and *H. opuntia* dwell among the *Thalassodendron*. *Caulerpa serrulata* and *C. cupressoides* inhabit bottoms of sandy depressions. Phytocoenoses of *T. ciliatum* with typical species composition were found on parts of the northeastern coast of the subtidal zone of St. Joseph Island (Fig. 25). *Halimeda* communities with rich species composition of associated algae dominate on the reef slope.

Cladophoropsis sundanensis, *Boodlea struveoides* and *Valonia aegagropila* form mats along the reef edge. Populations of *Turbinaria ornata*, *Lobophora variegata*, *Dictyosphaeria cavernosa*, *D. verluyssii*, *Dictyurus purpurascens*, *Rhipilia tomentosa* and *Udotea argentea* occur at depths of 3-5 m. Deeper to 35-38 m, rubble and blocks are covered with dense low growing populations of numerous red algae such as *Gelidiella myrioclada*, *Gelidium pusillum*, *Gelidiopsis scoparia*, *Polysiphonia* sp., *Lophosiphonia villum*, *Herposiphonia secunda* f. *tenella*, *Heterosiphonia crispella*, *Ceramium fastigiatum*, *Centroceras apiculatum*, *Hypnea spinella* and *Laurencia* sp. The green algae *Microdictyon okamurai*, *Struvea anastomosans*, *Caulerpa* sp., *Halimeda micronesica*, *H. stuposa*, *Valoniopsis pachynema* and *Valonia aegagropila* are the most frequent, while *Codium tomentosum*, *C. geppii*, *Cladophora laetevirens*, *Lophosiphonia reptabunda*, *Lomentaria mauritiana*, *L. hawaiiiana*, *Chondria dasyphylla*, *Jania decussatodichotoma* and *Halophila stipulacea* occur less frequently. *Anadyomene plicata*, *Scinaia* and *Gracilaria cylindrica* are occasional and sparsely distributed.

St. Joseph and D'Arros Islands contain 4 seagrasses and 120 algal species, including 69 Rhodophyta, 46 Chlorophyta, 4 Phaeophyta and 2 Cyanophyta.

Astove Atoll

As a rule, the intertidal zone of Astove Atoll is characterized by a mosaic structure of phytocoenoses and massive development of *Laurencia*. The intertidal and upper subtidal vegetative cover differs considerably from that of the other islands by its structure and species composition. There is a polydominant phytocoenosis of *Thalassodendron ciliatum* - *Caulerpa sertularioides* + *Acanthopora spicifera* formed on the vast silt-sand shallow area along the coast (Fig. 27; Table 2). In the lower horizon, this is replaced by a phytocoenosis formed by *T. ciliatum* and several *Laurencia*

species, including *L. decumbens* (Fig. 26, Sts. 247-249; Table 2). Maximal quantitative development of macrophytes occurs at the reef edge (Fig. 27), with associates consisting of *Laurencia parvipapillata*, *L. corymbosa*, *L. sp.*, *Liagora sp.*, *Hypnea spinella*, *Chaetomorpha crassa*, *Halimeda opuntia*, *Dictyosphaeria cavernosa*, *D. verluysii*, *Valonia aegagropila* and *Boodlea struveoides*.

Two phytocoenoses can be distinguished on the subtidal reef slope. A phytocoenosis of *Thalassodendron ciliatum* - *Halimeda hederacea* - *Laurencia sp.* occurs from 0-3 m in depth. Deeper, coral populations appear, and between them oligodominant phytocoenoses of *Halimeda copiosa* + *Caulerpa sp.* are located on sandy areas containing dead coral debris (Table 2). *Valonia aegagropila*, *Dictyosphaeria cavernosa*, *D. verluysii*, *Halimeda opuntia*, *H. tuna*, *Avrainvillea amadelpha f. submersa*, *Laurencia patentisamea*, *L. corymbosa* and *Gelidiella myrioclada* are commonly associated species (Fig. 28). The distinctive feature of the subtidal vegetation of Astove Island is the development of massive populations of *Caulerpa sp.* at 20-50 m depths. The benthic vegetation of Astove Island was not examined fully due to time constraints, so only 3 seagrasses and 61 algal species (32 red, 27 green and 2 brown algae) were found.

Mahé and adjacent islands

The northern, eastern and northeastern coasts of the island and three small islands just outside Victoria Harbor (Figs. 29-31) were studied. The intertidal zone of the northeastern coast is open to the sea and narrow (60-80 m), with a slight slope. A phytocoenosis of *Cladophoropsis sundanensis* + *Centroceras clavulatum*, along with the associated species *Ulva rigida*, *Cladophora socialis*, *Valonia aegagropila*, *Champia parvula*, *Cladophora patentiramea*, *Hypnea sp.* and *Jania sp.*, populate stone blocks in the middle intertidal horizon. An oligodominant association dominated by *Sargassum-Gracilaria multifurcata* occupies the lower intertidal horizon spreading almost to the reef-flat edge (Fig. 30; Table 2). *Gracilaria crassa* develops in shallow water habitats, deeper it is replaced by populations of *G. multifurcata*, *G. sp.*, *Amphiroa foliacea*, *Gelidiella acerosa*, *Jania capillacea* and *Cheilosporum spectabile*, forming mats. The species composition of the associated algae is rather rich with *Gelidiopsis scoparia*, *Hypnea valentiae*, *Laurencia papillosa*, *Sargassum cristaefolium*, *S. microcystum*, *Colpomenia sinuosa*, *Dictyopteris delicatula*, along with species of *Padina*, *Dictyota*, *Turbinaria* and *Sphacelaria* being found here.

Sargassum cristaefolium and *Turbinaria decurrens* occur on the fringing reef-flat of the northeast and east coasts and dominate on stony reef slope sites lacking corals in the subtidal zone (Fig. 29; Table 2; Sts. 164-167) where *Tricleocarpa oblongata* is a subdominant. Associates include *Hypnea valentiae*, *Ulva rigida*, *Caulerpa taxifolia*, *Cladophora patentiramea*, *Chlorodesmis comosa* and *Syringodium isoetifolium*.

Seagrass communities develop southwards into the harbor with *Cymodocea rotundata* inhabiting a narrow band along the shore, which is then replaced by *Thalassodendron ciliatum* occupying the entire area exposed at low waters. Associations of *Sargassum cristaefolium* occupy the southeastern coast's lower intertidal and upper subtidal zones (Figs. 29-31; Table 2). In the intertidal zone, the lower level of the *Sargassum* phytocoenosis includes *Gracilaria crassa*, *Cheilosporum spectabile*, *Jania longiartha*, *J. unguolata*, *Hypnea pannosa*, *H. nidulans*, *Laurencia parvipapillata*, *Amphiroa foliacea*, *Cladophoropsis sundanensis* and *Gelidiella acerosa*, which form mats. Isolated populations of *Dictyota indica*, *D. dichotoma*, *D. divaricata*, *Turbinaria ornata*, *Padina sp.* and *Caulerpa racemosa* occur as well.

Sargassum phytocoenoses have mono- and oligodominant structures ($H = 0-1, 1$), provide 100% cover and high biomass (Table 2). Minimal biomass was found in the upper intertidal zone while maximal biomass occurred near the reef edge (Fig. 30). The biomass of the various phytocoenoses

decreases with depth. At 8-10 m deep, *Sargassum* phytocoenoses are replaced by those dominated by *Halimeda*, which are distributed around the island in a form of belt, as well as *Sargassum* spp. Seagrass phytocoenoses, including *Thalassia hemprichii*, *Thalassodendron ciliatum*, *Halodule uninervis* and *Halophila ovalis*, develop on shallow sites in the middle intertidal horizon where they attain maximal biomass. *Sargassum* phytocoenoses of the subtidal zone include species such as *Turbinaria decurrens*, *Lobophora variegata*, *Dictyota indica*, *Padina* sp. and *Tricleocarpa oblongata*.

St. Anne Island

The association of *Sargassum polycystum* + *Turbinaria ornata* occupies the middle intertidal horizon of the south part of the island (Fig. 29), whereas in the lower horizon it is replaced by an association of *Sargassum cristaefolium*. The lower level of this association is made up of dense mats of *Amphiroa foliacea* and *Gelidiella acerosa*. *Thalassia hemprichii* and *Halodule uninervis* grow along this coast in small shallow bays, while *Halophila ovalis* occupies more silty sites. The lower border of the *Sargassum* phytocoenosis extends to a depth of 0.8-2 m. Coral populations occupy the bottom deeper.

Cerf Island

Sargassum microcystum and *S. cristaefolium* dominate the lower intertidal and upper subtidal zones. The main coenobiont of this community is *Turbinaria ornata*. The lower level is formed by *Amphiroa foliacea*, *Cheilosporum spectabile*, *Jania capillacea*, *Haliptilon subulatum*, *Gelidiella acerosa* and *Halimeda opuntia*. Populations of *Padina* sp., *Dictyota* sp. and *Cymodocea serrulata* occur rarely and near the shore. Dense mats of *Gelidiopsis scoparia* cover dead coral blocks among *Sargassum* spp. in the upper subtidal zone and *Cladophoropsis membranacea* grows on the sandy bottom among the blocks. Below 3-4 m in depth, *Sargassum* spp. communities are replaced by populations of coral.

Anonyme Island

The marine vegetation of the north side of Anonyme Island, situated at the south end of Victoria Harbor, was investigated. Monodominant continuous phytocoenoses of *Sargassum microcystum* + *S. cristaefolium* occupy sandy-stony bottoms at 0.5-1.2 m in depth (Fig. 29; Sts. 169-173; Table 2). The species composition of these phytocoenoses is limited and includes such species as *Hypnea nidulans*, *Jania capillacea*, *J. unguolata*, *Centroceras clavulatum*, *Leveillea jungermannioides*, *Sphacelaria rigidula*, *Gelidium pusillum*, *Chlorodesmis comosa*, *Acetabularia parvula*, *Bryopsis pennata* and *Gelidiella acerosa*. The north reef slope is exposed to wave action and consists of blocks with poorly developed vegetation (Fig. 12; Table 2; Sts. 173-175). *Turbinaria ornata*, *Lobophora variegata*, *Dasya baillouviana* and crustose algae occur rarely.

Near Mahé and its adjacent islands, 7 seagrasses and 173 algal species were collected, including 86 reds, 53 greens, 27 browns and 7 blue-greens.

Praslin Island

The marine vegetation of the eastern and central areas of Grande Anse Bay and the southern and southwestern coasts of Praslin were investigated to a depth of 40 m (Figs. 32-34). In the middle intertidal horizon of Grande Anse Bay, an association of *Gelidiella acerosa* is formed on separate rocky blocks, lower it is replaced by *Gracilaria crassa* associations. Sandy bottom sites between rocky

blocks are overgrown by *Sargassum ilicifolium*. Phytocoenoses of the seagrasses *Cymodocea serrulata* + *Syringodium isoetifolium* + *Thalassodendron ciliatum*, *S. isoetifolium* and *Halodule uninervis* are situated in the nearshore sandy intertidal zone. *Caulerpa serrulata* predominates in the association of *C. serrulata* + *S. isoetifolium* and is responsible for 60-70% of the biomass. From the lower intertidal border, to 1-1.2 m deep, the *T. ciliatum* association inhabits sandy to stony substrata (Table 2; Fig. 34). The width of the *T. ciliatum* belt reaches 800-1000 m. *Halimeda stuposa* is typically found in this association.

At shallow sites (0.3-0.5 m), the above seagrass belt is replaced by a phytocoenosis of *Sargassum cristaeifolium* - *Padina* sp. The species composition of this association is reduced and includes *Lobophora variegata*, *Dictyota indica* and *Chlorodesmis comosa*. With increasing depth, populations of *S. cristaeifolium* - *Padina* sp. are replaced by multiple *Sargassum* assemblages that extend down to 8-10 m in depth. Maximal cover and biomass are found between depths of 1 to 3 m (Table 2). The species composition of *Sargassum*-dominated phytocoenoses is diverse and includes *Caulerpa cupressoides*, *C. serrulata*, *C. racemosa*, *C. sertularioides*, *C. mexicana*, *C. taxifolia*, *C. ambigua*, *Dictyosphaeria cavernosa*, *Enteromorpha clathrata*, *Chlorodesmis cosmosa*, *Cladophoropsis sundanensis*, *Struvea anastomosans*, *Dictyopteris polypodioides*, *Dictyota indica*, *D. friabilis*, *D. divaricata*, *Lobophora variegata*, *Turbinaria conoides*, *Sphacelaria rigidula*, *S. tribuloides*, *Centroceras clavulatum*, *C. apiculatum*, *Gelidiopsis scoparia*, *Gelidiella acerosa*, *Champia parvula*, *Tolypocladiella glomerulata* and *Wurdemannia miniata*.

Below 9 m, the bottom is sandy with large calcium carbonate blocks and coral colonies. Hard substrata are overgrown with crustose and small algae such as *Gelidiella lubrica*, *Ceramium fastigiatum*, *Lophosiphonia villum*, *Gelidium pusillum* and *Champia parvula*. Among the larger macroalgae, *Lobophora variegata* and *Laurencia* species are the most frequent.

At the 40 m depth, *Chlorodesmis comosa*, *Cladophora laetevirens*, *Halimeda* sp., *Cladophoropsis sundanensis*, *Dictyota divaricata*, *Champia salicornioides*, *Dasya* sp., *Antithamnion herminieri* and *Chondria* sp. are common.

La Digue Island

The eastern intertidal zone is exposed to strong wave action and is narrow and devoid of vegetation, whereas the western coast is more protected from wave effects. The upper and middle intertidal horizons consist of a sandy beach. Algae overgrow sandy-stony reef-flat habitats. The oligodominant association of *Thalassodendron ciliatum* - *Hypnea pannosa* occurs near the shoreline (Table 2; St. 180; Fig. 34) and includes *Turbinaria ornata*, which deeper forms a 15-20 m wide belt. *Sargassum turbinarioides* dominates the middle of the reef-flat (Table 2). Distinctive phytocoenoses develop at lower levels, consisting mainly of *Hypnea nidulans* and *H. pannosa* mats which provide up to 8-20% of the total biomass. Populations of *Heterosiphonia* sp. often occur along the edge of the reef-flat among the *Sargassum* phytocoenoses. In the subtidal zone, *Sargassum* phytocoenoses extend down to 8 m in depth. Deeper, down to 30-31 m, there is a belt of crustose algae with mats of small red algae and separate patches of *Lobophora variegata* and *Laurencia* sp. The species composition of algae in this region is similar to that of deep waters off Praslin Island.

Phytocoenoses of granitic islands tend to have oligodominant structures, considerable biomass and limited species composition of associated species. *Sargassum* communities have monodominant structure, great biomass and rich species composition, which all become reduced with depth.

Near Praslin and La Digue Islands, 6 seagrass and 136 algal species, including 72 red, 35 green, 22 brown and 7 blue-green species were recorded.

CONCLUSIONS

The benthic vegetation of the Seychelles Islands shows several common characteristics, presumably related to similar geomorphological features of the coastal zones and the tropical oceanic location of the islands:

1. Rich species composition of algae at every island.
2. Wide range of vertical distribution of most the macrophyte species.
3. Domination of red (45-64.2%) and green (25.5-42.4%) algal species and poor development of brown algae (2.5-16.1%) in the floras of the low carbonate islands.
4. A great number of genera are common to all islands surveyed: green algae - *Caulerpa*, *Halimeda*, *Microdictyon*, *Boodlea*, *Anadyomene*, *Cladophoropsis*, *Avrainvillea*, *Udotea*, *Acetabularia*, *Valonia*, *Dictyosphaeria* and *Struvea*; brown algae - *Lobophora*, *Turbinaria* and *Dictyopteris*; red algae - *Galaxaura*, *Gelidiella*, *Wurdemannia*, *Peyssonnelia*, *Jania*, *Melobesia*, *Hypnea*, *Champia*, *Haloplegma*, *Anotrichium*, *Chondria*, *Centroceras*, *Dasya*, *Heterosiphonia*, *Lophocladia*, *Herposiphonia* and *Laurencia*; and the seagrasses - *Thalassia* and *Thalassodendron*.
5. *Thalassodendron ciliatum* and *Thalassia hemprichii* dominate the overall vegetative cover of soft bottoms. In the middle and lower intertidal horizons, seagrasses occur in the following sequence: *Halophila ovalis* - *Halodule uninervis* - *Thalassia hemprichii* - *Cymodocea serrulata* - *C. rotundata* - *Syringodium isoetifolium* - *T. ciliatum*. *Thalassodendron ciliatum* consistently forms a belt that dominates in the subtidal zone.
6. *Thalassodendron ciliatum* plays an important role in the stabilization of unconsolidated substrata in the coastal ecosystems of the atoll islands.
7. The benthic vegetation is characterized by relatively high standing stocks. In habitats with highly developed vegetative cover approaching 100%, the biomass reaches $2-4 \text{ kg} \cdot \text{m}^{-2}$. Maximal biomass was found over the depth range of 0.5-0.3 m, and averaged $4-8 \text{ kg} \cdot \text{m}^{-2}$.
8. Commercially exploitable stocks of macrophytes were found: mainly *Thalassodendron ciliatum* (biomass = $1-4 \text{ kg} \cdot \text{m}^{-2}$) on atoll island sand and on the granitic islands, primarily species of *Sargassum* (biomass = $2-10 \text{ kg} \cdot \text{m}^{-2}$) and *Gracilaria* (biomass = $2-6 \text{ kg} \cdot \text{m}^{-2}$).

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Table 1. Preliminary checklist of benthic marine algae and seagrasses collected near Seychelles Islands. M = Mahé, P = Praslin, Co = Coëtivy, F = Farquhar, D = Desroches, A = Aldabra, AB = African Banks, S = St. Joseph, Pd = Providence, Cs = Cosmoledo and As = Astove.

Taxon	Island										
	Co	F	A	D	P	M	AB	S	Pd	Cs	As
CYANOPHYTA											
Oscillatoriales											
Oscillatoriaceae											
1. <i>Oscillatoria margaritifera</i> (Kütz.) Gom.					P	M	AB				
2. <i>Oscillatoria miniata</i> (Zanard.) Hauck					P	M					
3. <i>Lyngbya confervoides</i> Ag.					P	M	AB				
4. <i>Lyngbya majuscula</i> (Dillw.) Harv.		F	A	D	P	M	AB	S			
5. <i>Lyngbya martensiana</i> Menegh.		F	A			M					
6. <i>Lyngbya</i> sp.		F				M		S			
7. <i>Symploca hydroides</i> (Harv.) Kütz.					P						
Nostocales											
Rivulariaceae											
8. <i>Calothrix confervicola</i> (Dillwyn) Ag.						M					
9. <i>Calothrix aeruginea</i> (Kütz.) Thuret					P						
Nostocaceae											
10. <i>Calothrix parietina</i> (Näg. ex Kütz.) Thuret					P						
Nostocales											
11. <i>Hormothamnium solutum</i> Born. et Grunow	Co			D							
RHODOPHYTA											
Goniotrichales											
Goniotrichaceae											
12. <i>Chroodactylon ornatum</i> (C. Ag.) Basson (= <i>Asterocytis ornata</i> ; <i>Asterocytis ramosa</i>)		F	A	D		M	AB	S			
13. <i>Stylonema alsidii</i> (Zanard.) Drew		F	A	D	P	M	AB	S		Cs	
Bangiales											
Erythropeltidaceae											
14. <i>Erythrotrichia carnea</i> (Dillw.) J. Ag.	Co	F	A				AB	S	Pd	Cs	
15. <i>Erythrocladia</i> sp.						M					
Florideophyceae											
Acrochaetiales											
Acrochaetiaceae											
16. <i>Acrochaetium occidentale</i> Børg.				D							
17. <i>Acrochaetium robustum</i> Børg.						M					
18. <i>Acrochaetium seriatum</i> Børg.					P	M					
19. <i>Acrochaetium</i> sp.	Co										
20. <i>Chromastrum crassipes</i> (Børg.) Papenf. (= <i>Acrochaetium crassipes</i>)						M					

Table 1. Continued.

Taxon	Island										
	Co	F	A	D	P	M	AB	S	Pd	Cs	As
Nemaliales											
Liagoraceae											
21. <i>Liagora ceranoides</i> Lam.		F	A					S			
22. <i>Liagora divaricata</i> Tseng	Co										
23. <i>Liagora pinnata</i> Harv.				D							
24. <i>Liagora</i> sp.1		F									
25. <i>Liagora</i> sp.2	Co										
26. <i>Liagora</i> sp.3											As
Galaxauraceae											
27. <i>Scinaia complanata</i> (Collins) Cotton								S			
28. <i>Galaxaura marginata</i> (Ell. et Sol.) Lam.				D							
29. <i>Tricleocarpa oblongata</i> (Ell. et Sol.) Huisman et Borowitzka (= <i>Galaxaura oblongata</i>)	Co	F	A		P	M			Pd		
30. <i>Galaxaura rugosa</i> (Ellis et Soland.) Lam. (= <i>Galaxaura rudis</i>)	Co	F	A	D	P	M			Pd	Cs	
31. <i>Galaxaura</i> sp.				D					Pd		
Gelidiales											
Gelidiaceae											
32. <i>Gelidium crinale</i> f. <i>corymbosa</i> (Kütz.) J. Feldm. et Hamel						M					
33. <i>Gelidium pusillum</i> (Stackh.) Le Jolis	Co	F	A	D	P	M		S		Cs	
34. <i>Pterocladia caloglossoides</i> (Howe) Daws.					P						
Gelidiellaceae											
35. <i>Gelidiella acerosa</i> (Forsskål) J. Feldm. et Hamel					P	M				Cs	As
36. <i>Gelidiella adnata</i> Daws.	Co	F	A		P	M				Cs	As
37. <i>Gelidiella lubrica</i> (Kütz.) J. Feldm. et Hamel	Co	F	A	D	P	M	AB				
38. <i>Gelidiella myrioclada</i> J. Feldm. et Hamel	Co	F	A	D	P		AB	S		Cs	As
39. <i>Gelidiella sanctarum</i> J. Feldm. et Hamel	Co										
40. <i>Gelidiella pannosa</i> J. Feldm. et Hamel (= <i>Gelidiella tenuissima</i>)	Co	F	A		P	M	AB	S			
Bonnemaisoniales											
Bonnemaisoniaceae											
41. " <i>Falkenbergia hillebrandii</i> " (N.B. - stage of <i>Asparagopsis</i>)	Co	F		D	P	M					
Corallinales											
Corallinaceae											
42. <i>Fosliella farinosa</i> (Lam.) Howe					P	M		S		Cs	
43. <i>Neogoniolithon</i> sp.								S	Pd	Cs	As
44. <i>Pheophyllum confervicola</i> (Kütz.) Chamb. (= <i>Melobesia minutula</i>)					P						
45. <i>Hydrolithon breviclavium</i> (Fosl.) Fosl.										Cs	
46. <i>Porolithon gardineri</i> (Fosl.) Fosl.		F	A				AB		Pd	Cs	
47. <i>Spongites reinboldii</i> (W.v. Bosse et Fosl.) Penrose et Woelkerling					P						

Table 1. Continued.

Taxon	Island										
	Co	F	A	D	P	M	AB	S	Pd	Cs	As
48. <i>Melobesia</i> sp.	Co	F	A	D	P	M			Pd	Cs	
49. <i>Mesophyllum mesomorphum</i> (Fosl.) Adey							AB		Pd	Cs	
50. <i>Sporolithon ptychoides</i> Heydrich (= <i>Spongites erythraeum</i>)					P	M					
51. <i>Spongites sporolithon</i>					P	M		S	Pd		
52. <i>Lithophyllum kotschianum</i> (Fosl.)					P	M					
53. <i>Cheilosporum spectabile</i> Harv.						M			Pd		
54. <i>Halitilton subulatum</i> (Ell. et Sol.) Johan.				D							
55. <i>Jania adhaerens</i> Lam.	Co	F	A								
56. <i>Jania capillacea</i> Harv.	Co	F	A	D	P	M	AB	S	Pd	Cs	As
57. <i>Jania decussato-dichotoma</i> (Yendo) Yendo								S		Cs	As
58. <i>Jania longiartha</i> Daws.	Co					M					
59. <i>Jania unguolata</i> (Yendo) Yendo f. <i>brevior</i> (Yendo) Yendo	Co	F	A	D	P	M	AB		Pd	Cs	
60. <i>Jania</i> sp.				D		M		S			
61. <i>Amphiroa anastomosans</i> W.v. Bosse				D							
62. <i>Amphiroa foliacea</i> Lam.						M					
63. <i>Amphiroa fragilissima</i> (L.) Lam.						M		S			
64. <i>Metagoniolithon stelligerum</i> (Lam.) W.v. Bosse Cryptonemiales Peyssonneliaceae	Co	F			P						
65. <i>Peyssonnelia dubyi</i> Crouan										Cs	
66. <i>Peyssonnelia</i> sp.1	Co	F	A	D	P	M		S	Pd	Cs	As
67. <i>Peyssonnelia</i> sp.2 Dumontiaceae									Pd	Cs	
68. <i>Dudresnaya</i> sp.				D							
69. <i>Gibsmithia hawaiiensis</i> Doty Halymeniaceae					P						
70. <i>Halymenia</i> sp. Kallymeniaceae				D	P	M					
71. <i>Kallymenia</i> sp. Gigartinales Gymnophlocaceae	Co	F									
72. <i>Titanophora</i> sp.										Cs	
73. <i>Portieria hornemannii</i> (Lyngbye) Silva Hypneaceae				D							
74. <i>Hypnea cenomyce</i> J. Ag.					P						
75. <i>Hypnea cervicornis</i> J. Ag.						M					
76. <i>Hypnea cornuta</i> (Kütz.) J. Ag.					P	M					
77. <i>Hypnea esperi</i> Bory	Co	F	A	D	P	M		S	Pd		As
78. <i>Hypnea nidulans</i> Setchell					P	M	AB			Cs	
79. <i>Hypnea pannosa</i> J. Ag.	Co	F	A	D	P	M					As
80. <i>Hypnea spinella</i> (C. Ag.) Kütz.		F	A	D	P	M		S	Pd	Cs	As
81. <i>Hypnea valentiae</i> (Turn.) Mont.				D	P					Cs	As
82. <i>Hypnea</i> sp.		F	A					S			As

Table 1. Continued.

Taxon	Island										
	Co	F	A	D	P	M	AB	S	Pd	Cs	As
Plocamiaceae											
83. <i>Plocamium</i> sp.		F		D		M		S	Pd		As
Caulacanthaceae											
84. <i>Caulacanthus</i> sp.					P						
Wurdemanniaceae											
85. <i>Wurdemannia miniata</i> (Sprengel) J. Feldm. et Hamel		F	A		P	M	AB	S		Cs	As
Phylloporaceae											
86. <i>Gymnogongrus chnoosporoides</i> Tan. et Pham-Hoang									Pd		
87. <i>Gymnogongrus pygmaeus</i> J. Ag.		F									
Gigartinaceae											
88. <i>Gigartina</i> sp.	Co		A			M					
Gracilariaceae											
89. <i>Gracilaria crassa</i> Harv.			A			M	AB				
90. <i>Gracilaria cylindrica</i> Børg.			A		P	M		S			As
91. <i>Gracilaria multifurcata</i> Børg.						M					
92. <i>Gelidiopsis gracilis</i> (Kütz.) Vickers					P						
93. <i>Gelidiopsis scoparia</i> (Mont. et Mill.) Schmitz					P	M					As
94. <i>Gelidiopsis</i> sp.		F									
95. <i>Ceratodictyon spongiosum</i> Zanard.		F	A								
Rhodymeniales											
Rhodymeniaceae											
96. <i>Botryocladia skottsbergii</i> (Børg.) Levr.	Co	F	A	D	P	M	AB	S		Cs	As
97. <i>Chrysomenia enteromorpha</i> Harv.									Pd		
98. <i>Chrysomenia pyriformis</i> Børg.	Co						AB	S			
99. <i>Chrysomenia</i> sp.	Co	F	A								
100. <i>Coelarthrum boergesenii</i> W.v. Bosse	Co	F	A	D			AB	S	Pd		
101. <i>Rhodymenia anastomosans</i> W.v. Bosse				D							
102. <i>Rhodymenia</i> sp.						M					
Lomentariaceae											
103. <i>Lomentaria corallicola</i> Børg.				D	P						
104. <i>Lomentaria mauritiana</i> Børg.				D	P	M	AB	S	Pd		
Champiaceae											
105. <i>Champia globulifera</i> Børg.				D		M					
106. <i>Champia indica</i> Børg.											As
107. <i>Champia parvula</i> (C. Ag.) Harv.	Co	F	A	D	P	M	AB	S	Pd	Cs	As
108. <i>Champia salicornoides</i> Harv.				D	P	M		S	Pd		
109. <i>Champia viellardii</i> Kütz.		F	A			M					
110. <i>Champia</i> sp.				D				S			
Ceramiales											
Ceramaceae											
111. <i>Crouania attenuata</i> (C. Ag.) J. Ag.			A	D			AB	S	Pd		
112. <i>Antithamnion lherminieri</i> Nasr.	Co			D							
113. <i>Antithamnion</i> sp.			A	D		M	AB	S		Cs	

Table 1. Continued.

Taxon	Island											
	Co	F	A	D	P	M	AB	S	Pd	Cs	As	
154. <i>Heterosiphonia crispella</i> (C. Ag.) Wynne (= <i>Heterosiphonia wurdemannii</i>)	Co	F	A	D	P	M	AB	S	Pd	Cs		
155. <i>Heterosiphonia</i> sp.1	Co		A	D	P			S		Cs	As	
156. <i>Heterosiphonia</i> sp.2	Co	F	A				AB					
157. <i>Dictyurus purpurascens</i> Bory Rhodomelaceae	Co	F	A	D	P		AB	S	Pd	Cs	As	
158. <i>Polysiphonia coacta</i> Tseng	Co	F										
159. <i>Polysiphonia mollis</i> J. Hook. et Harv.					P	M	AB	S				
160. <i>Polysiphonia ferulacea</i> Suhr ex J. Ag.					P							
161. <i>Polysiphonia scopulorum</i> Harv.	Co											
162. <i>Polysiphonia subtilissima</i> Mont.		F	A	D								
163. <i>Polysiphonia</i> sp.	Co	F	A	D	P	M	AB			Cs		
164. <i>Vidalia</i> sp.	Co	F		D				S				
165. <i>Tolypocladia glomerulata</i> (Ag.) Schmitz					P	M				Cs		
166. <i>Lophocladia trichoclados</i> (C. Ag.) Schmitz	Co	F	A	D	P	M	AB	S	Pd		As	
167. <i>Bostrychia binderi</i> Harv.						M						
168. <i>Herposiphonia secunda</i> (C. Ag.) Ambronn f. <i>tenella</i> (Ag.) Wynne	Co		A									
	Co	F	A	D	P	M	AB	S	Pd	Cs	As	
169. <i>Leveillea jungermannioides</i> (Hering et Martens) Harv.					P	M			Pd	Cs		
170. <i>Lophosiphonia reptabunda</i> (Suhr.) Kyl.	Co	F			P			S		Cs		
171. <i>Lophosiphonia villum</i> (J. Ag.) Setch. et Gardn.	Co	F	A	D	P	M	AB	S		Cs		
172. <i>Lophosiphonia</i> sp.										Cs		
173. <i>Chondria dasyphylla</i> (Woodw.) C. Ag.			A					S				
174. <i>Chondria polyrhiza</i> Coll. et Herv.			A									
175. <i>Chondria repens</i> Børg.	Co	F			P	M	AB	S	Pd	Cs		
176. <i>Chondria</i> sp.		F	A							Cs		
177. <i>Acanthophora spicifera</i> (Vahl) Børg.			A			M					As	
178. <i>Laurencia articulata</i> Tseng					P							
179. <i>Laurencia corymbosa</i> J. Ag.									Pd	Cs	As	
180. <i>Laurencia decumbens</i> Kütz.		F	A	D	P			S		Cs	As	
181. <i>Laurencia distichophylla</i> J. Ag.			A					S				
182. <i>Laurencia obtusa</i> (Huds.) Lam.	Co	F				M						
183. <i>Laurencia patentiramea</i> (Montagne) Kütz.	Co	F	A			M	AB	S		Cs	As	
184. <i>Laurencia parvipapillata</i> Tseng.	Co	F	A	D		M		S	Pd	Cs	As	
185. <i>Laurencia papillosa</i> (Ag.) Grev.		F	A	D	P	M		S	Pd	Cs	As	
186. <i>Laurencia pygmaea</i> W.v. Bosse			A			M						
187. <i>Laurencia</i> sp.1	Co	F	A				AB	S			As	
188. <i>Laurencia</i> sp.2						M						
189. <i>Laurencia</i> sp.3			A			M						
190. <i>Laurencia</i> sp.4					P							
191. <i>Laurencia</i> sp.5				D	P		AB	S				

Table 1. Continued.

Taxon	Island										
	Co	F	A	D	P	M	AB	S	Pd	Cs	As
PHAEOPHYTA											
Ectocarpales											
Ectocarpaceae											
192. <i>Ectocarpus</i> sp.						M					
193. <i>Hincksia mitchelliae</i> (Harv.) Silva				D		M					
194. <i>Hincksia breviarticulata</i> (J. Ag.) Silva						M					
195. <i>Streblonema</i> sp.					P						
Scytosiphonales											
Scytosiphonaceae											
196. <i>Colpomenia sinuosa</i>					P	M					
(Mert. ex Roth) Derb. et Sol.											
197. <i>Hydroclathrus clathratus</i> (C. Ag.) Howe						M					
198. <i>Rosenvingea intricata</i> (J. Ag.) Børg.						M					
Chnoosporaceae											
199. <i>Chnoospora minima</i> (Hering) Papenf.						M					
Sphacelariales											
Sphacelariaceae											
200. <i>Sphacelaria rigidula</i> Kütz.		F	A		P	M	AB			Cs	
201. <i>Sphacelaria tribuloides</i> Menegh.	Co				P	M				Cs	
Dictyotales											
Dictyotaceae											
202. <i>Dictyota bartayresii</i> Lam.			A	D	P						
203. <i>Dictyota ceylanica</i> Kütz.					P						
204. <i>Dictyota divaricata</i> Lam.					P						
205. <i>Dictyota friabilis</i> Setch.			A		P						
206. <i>Dictyota indica</i> Sond. ex Kütz.					P	M					
207. <i>Dictyota patens</i> J. Ag.						M					
208. <i>Dictyota</i> sp.						M		S			
209. <i>Dictyopteris delicatula</i> Lam.	Co	F		D	P	M		S	Pd		
210. <i>Dictyopteris polyposioides</i> (DeCandalle) Lam.					P	M					
211. <i>Padina minor</i> Yam.		F									
212. <i>Padina pavonica</i> (L.) Thivy					P	M					
213. <i>Padina</i> sp.					P						
214. <i>Lobophora variegata</i> (Lam.) Womers.	Co	F	A	D	P	M	AB	S	Pd	Cs	As
Fucales											
Cystoseiraceae											
215. <i>Hormophysa cuneiformis</i> (Gmelin) Silva						M					
Sargassaceae											
216. <i>Sargassum cristaefolium</i> C. Ag.		F				M					
217. <i>Sargassum ilicifolium</i> (Turn.) C. Ag.		F				M					
218. <i>Sargassum mcclurei</i> Setch.					P	M					
219. <i>Sargassum microcystum</i> J. Ag.					P	M					
220. <i>Sargassum piluliferum</i> (Turner) C. Ag.					P						

Table 1. Continued.

Taxon	Co	F	A	D	Island		AB	S	Pd	Cs	As
					P	M					
221. <i>Sargassum polycystum</i> C. Ag.						M					
222. <i>Sargassum turbinarioides</i> Grun.					P	M					
223. <i>Sargassum</i> sp.					P						
224. <i>Turbinaria conoides</i> (J. Ag.) Kütz.			A		P	M					
225. <i>Turbinaria decurrens</i> Bory						M	AB				
226. <i>Turbinaria ornata</i> (Turn.) J. Ag.	Co	F	A	D	P	M		S		Cs	As
227. <i>Turbinaria</i> sp.					P					Cs	

CHLOROPHYTA

Phaeophilales

Phaeophilaceae

228. *Phaeophila dendroides* (P. et H. Crouan) Batt. Co

Dasycladales

Dasycladaceae

229. *Neomeris annulata* Dickie A Cs As230. *Neomeris bilimbata* Koster D231. *Neomeris vanbosseae* Howe A Pd Cs232. *Neomeris* sp. D

Polyshysacaea

233. *Polyphysa* sp. A D234. *Acetabularia clavata* Yam. Co A D M235. *Acetabularia exigua* Solms-Laub. Co M236. *Acetabularia parvula* Solms-Laub. Co A D P M Cs237. *Acetabularia pusilla* (Howe) Collins A D P M Cs238. *Acetabularia* sp. Co

Bryopsidales

Caulerpaceae

239. *Caulerpa brachypus* Harv. Cs As240. *Caulerpa cupressoides* (Vahl) Ag. Co F A D P AB S Pd Cs As241. *Caulerpa cupressoides* var. *mamillosa* F D P Cs

(Mont.) W.v. Bosse

242. *Caulerpa fastigiata* Mont. F243. *Caulerpa mexicana* Sond. ex Kütz. F A D P S244. *Caulerpa microphysa* (W.v. Bosse) J. Feldm. P M245. *Caulerpa peltata* Lam. F A P M As246. *Caulerpa racemosa* (Forsskål) J. Ag. Co F P M Asvar. *macrophysa* (Sond. ex Kütz.) W. Taylor F Csvar. *occidentalis* (J. Ag.) Børg. Csvar. *peltata* (Lam.) Eubank Co P M247. *Caulerpa serrulata* (Forsskål) J. Ag. Co F A D P M S Cs Asvar. *serrulata* f. *spiralis* (W.v. Bosse) Gilbert F S Cs As248. *Caulerpa setularioides* (Gmel.) Howe Co P M AB S Cs Asf. *farlowii* (W.v. Bosse) Børg. Cs As

Table 1. Continued.

Taxon	Island										
	Co	F	A	D	P	M	AB	S	Pd	Cs	As
249. <i>Caulerpa taxifolia</i> (Vahl) C. Ag.	Co	F	A		P	M		S			
250. <i>Caulerpa ambigua</i> Okam.					P	M		S		Cs	
251. <i>Caulerpa webbiana</i> Mont.										Cs	
252. <i>Caulerpa</i> sp.1	Co	F									
253. <i>Caulerpa</i> sp.2			A								
254. <i>Caulerpa</i> sp.3	Co			D	P		AB	S	Pd		As
Udoteaceae											
255. <i>Chlorodesmis comosa</i> Harv. et Bail.	Co	F	A	D	P	M		S		Cs	
256. <i>Boodleopsis pusilla</i> (Collins) W. Taylor, Joly et Bernatowicz			A	D	P		AB				
257. <i>Avrainvillea amadelpha</i> f. <i>submersa</i> Gepp	Co	F	A	D		M	AB	S	Pd	Cs	As
258. <i>Tydemania gardineri</i> A. et B. Gepp							AB	S			
259. <i>Rhipiliopsis reticulata</i> (van den Hoek) Farghaly	Co			D						Cs	
260. <i>Rhipilia tomentosa</i> Kütz.	Co	F		D			AB	S		Cs	As
261. <i>Udotea argentea</i> Zanard.	Co	F		D		M	AB	S			
262. <i>Udotea flabellum</i> (Ell. et Sol.) Howe	Co			D							
263. <i>Udotea javensis</i> (Mont.) A. Gepp et E. Gepp				D		M					
264. <i>Udotea orientalis</i> A. Gepp et E. Gepp	Co	F		D		M	AB	S	Pd		
Halimedaceae											
265. <i>Halimeda gracilis</i> Harv. ex J. Ag.	Co	F	A	D		M	AB	S	Pd	Cs	As
266. <i>Halimeda copiosa</i> Goreau et Graham	Co		A				AB	S		Cs	As
267. <i>Halimeda macroloba</i> Decne.		F	A	D	P	M	AB	S			
268. <i>Halimeda micronesica</i> Yam.	Co	F	A	D			AB	S	Pd		
269. <i>Halimeda opuntia</i> (L.) Lam.	Co	F	A	D	P	M	AB	S			As
270. <i>Halimeda stuposa</i> W. Taylor	Co	F	A	D			AB	S		Cs	
271. <i>Halimeda tuna</i> (Ell. et Sol.) Lam.	Co	F	A	D			AB	S	Pd	Cs	As
272. <i>Halimeda</i> sp.			A	D	P		AB	S			
Codiaceae											
273. <i>Codium formosanum</i> Yam.						M					
274. <i>Codium geppii</i> O.C. Schmidt								S			
275. <i>Codium tomentosum</i> (Huds.) Stackh.						M		S			
276. <i>Codium</i> sp.						M					
Bryopsidaceae											
277. <i>Derbesia marina</i> (Lyngb.) Solier		F	A			M					
278. <i>Derbesia</i> sp.					P						
279. <i>Halicystis ovalis</i> (Lyngb.) Aresch. (N.B. - sporophyte stage of <i>Derbesia marina</i>)						M					
280. <i>Bryopsis pennata</i> Lam.			A	D	P	M					
281. <i>Trichosolen</i> sp.								S			
Siphonocladales											
Valoniaceae											
282. <i>Valonia aegagropila</i> C. Ag.	Co	F		D		M	AB	S	Pd	Cs	As
283. <i>Valonia fastigiata</i> Harv. es J. Ag.				D		M	AB	S	Pd		
284. <i>Valonia utricularis</i> (Roth) Ag. f. <i>crustacea</i> Kuck.	Co			D				S		Cs	Cs

Table 1. Continued.

Taxon	Island										
	Co	F	A	D	P	M	AB	S	Pd	Cs	As
285. <i>Ventricaria ventricosa</i> (J. Ag.) Olsen et West		F	A			M				Cs	
286. <i>Dictyosphaeria cavernosa</i> (Forsskål) Børg.	Co	F	A	D	P	M	AB	S	Pd	Cs	As
287. <i>Dictyosphaeria versluysii</i> W.v. Bosse	Co	F	A	D	P	M	AB	S		Cs	As
288. <i>Valoniopsis pachynema</i> (Mart.) Børg.	Co			D			AB	S		Cs	As
Siphonocladaceae											
289. <i>Boergesenia forbessii</i> (Harv.) J. Feldm.			A			M	AB			Cs	
290. <i>Siphonocladus rigidus</i> Howe	Co			D		M			Pd	Cs	As
291. <i>Siphonocladus tropicus</i> (P. et H. Crouan) J. Ag.				D				S			
292. <i>Cladophoropsis herpestica</i> (Mont.) Howe					P	M					
293. <i>Cladophoropsis membranacea</i> (Ag.) Børg.						M	AB	S		Cs	
294. <i>Cladophoropsis modonensis</i> (Kütz.) Børg.					P	M					
295. <i>Cladophoropsis sundanensis</i> Reinb.	Co	F	A	D	P	M	AB	S		Cs	
Boodleaceae											
296. <i>Boodlea composita</i> (Harv.) Brand	Co			D				S			
297. <i>Boodlea siamensis</i> Reinb.				D							
298. <i>Boodlea struveoides</i> Howe	Co	F	A	D	P	M	AB	S	Pd	Cs	As
299. <i>Boodlea</i> sp.								S			
300. <i>Struvea anastomosans</i> (Harv.) Picc. et Grun.	Co	F	A	D	P	M	AB	S			
301. <i>Struvea elegans</i> Børg.		F			P				Pd		
302. <i>Struvea</i> sp.1	Co			D	P						
303. <i>Struvea</i> sp.2	Co										
Anadyomnaceae											
304. <i>Microdictyon okamurae</i> Setch.	Co	F	A	D		M	AB	S	Pd	Cs	As
305. <i>Microdictyon montagnei</i> Harv.	Co							S	Pd	Cs	
306. <i>Microdictyon</i> sp.	Co		A					S			
307. <i>Anadyomene plicata</i> C. Ag.							AB				
308. <i>Anadyomene wrightii</i> Harv. ex J.E. Gray	Co	F	A	D			AB	S	Pd	Cs	As
Cladophoraceae											
309. <i>Cladophora vagabunda</i> (L.) van den Hoek						M					
310. <i>Cladophora laetevirens</i> (Dillw.) Kütz.	Co				P	M		S		Cs	
311. <i>Cladophora patentiramea</i> (Mont.) Kütz.						M		S			
312. <i>Cladophora socialis</i> Kütz.		F				M				Cs	
313. <i>Cladophora</i> sp.			A			M					
314. <i>Rhizoclonium implexum</i> (Dillw.) Kütz. (= <i>Rhizoclonium kernerii</i>)		F				M		S			
315. <i>Chaetomorpha ligustica</i> (Kütz.) Børg.	Co					M				Cs	As
316. <i>Chaetomorpha crassa</i> (C. Ag.) Kütz.	Co	F				M					As
Chaetophorales											
Ulvellaceae											
317. <i>Entocladia</i> sp.		F									
318. <i>Phaeophila dendroides</i> (P. and H. Crouan) Batt.					P					Cs	
Ulvaes											
Ulvaceae											
319. <i>Enteromorpha clathrata</i> (Roth) Grev.	Co		A	D	P	M	AB			Cs	
320. <i>Enteromorpha flexuosa</i> (Wulf.) J. Ag.				D							

Table 1. Continued.

Taxon	Island										
	Co	F	A	D	P	M	AB	S	Pd	Cs	As
321. <i>Enteromorpha intestinalis</i> (L.) Link ex Nees				D	P	M					
322. <i>Enteromorpha kylinii</i> Bliding	Co	F	A	D		M					
323. <i>Enteromorpha linza</i> (L.) J. Ag.					P						
324. <i>Enteromorpha ralfsii</i> Harv.			A			M					
325. <i>Enteromorpha</i> sp.				D							
326. <i>Ulva rigida</i> C. Ag.	Co	F	A			M		S			As
SPERMATOPHYTA											
Potamogetonaceae											
1. <i>Halodule uninervis</i> (Forsskål) Aschers.	Co		A		P	M				Cs	As
2. <i>Cymodocea rotundata</i> Ehrenb. and Hemprich ex Aschers.					P	M				Cs	
3. <i>Cymodocea serrulata</i> (R. Br.) Aschers. et Magnus					P	M					
4. <i>Syringodium isoetifolium</i> (Aschers.) Dandy	Co		A		P	M					
5. <i>Thalassodendron ciliatum</i> (Forsskål) den Hartog	Co	F	A	D	P	M	AB	S	Pd	Cs	As
Hydrocharitaceae											
6. <i>Thalassia hemprichii</i> (Ehrenb.) Aschers.	Co	F	A	D		M	AB	S	Pd	Cs	As
7. <i>Halophila ovalis</i> (R. Br.) Hooker f. <i>hawaiiiana</i> (Doty et Stone) den Hartog				D		M		S			
8. <i>Halophila stipulacea</i> (Forsskål) Aschers.							AB	S			

Table 2. Quantitative characteristic of bottom vegetation of the Seychelles Islands (12 January - 12 March, 1989). In zone heading, "mih" = middle intertidal horizon, "lih" = lower intertidal horizon. "s" = sand, "st" = stones, "c" = corals, "cd" = coral debris and "Hs" = *Halimeda* sand.

Coast	Station	Depth in m, zone	Substrate	# of species	Biomass, g·m ⁻²	% cover	Growth height	Association	H
Cœtivy Island									
N-W	1	mih	s, cd, st	-	6	5	-	<i>Enteromorpha kylinii</i>	
N-W	2	mih	s, cd	1308	1327	100	15	<i>Thalassia hemprichii</i>	0
N-W	3	mih	s, cd	1768	424	100	10	<i>Halodule uninervis</i> + <i>Thalassia hemprichii</i>	0.90
N-W	4	mih	s, cd	1332	652	70	6	<i>Halodule uninervis</i> + <i>Thalassia hemprichii</i>	0
N-W	5	lih	s, cd,	720	1645	80	15	<i>Thalassodendron</i> - <i>Halimeda</i> + <i>Hypnea</i>	1.76
N-W	6	lih	s, cd,	3532	6631	100	20	<i>Thalassodendron</i> - <i>Halimeda</i> - <i>Dictyurus</i>	0.56
S	7	mih	s, cd,	1872	3306	90	20	<i>Thalassodendron</i>	0
S	8	mih	s, cd,	524	470	100	15	<i>Thalassia-Caulerpa</i>	0.39
S	9	lih	s, cd,	-	3442	100	10	<i>Halimeda</i> + <i>Dictyurus</i> + <i>Laurencia</i>	1.68
S	10	mih	s, cd	692	588	90	15	<i>Thalassia</i> + <i>Thalassodendron</i>	0.55
S	11	mih	s, cd,	408	3276	90	20	<i>Halimeda</i> + <i>Thalassodendron</i> <i>ciliatum</i> - <i>Laurencia</i>	1.30
N	12	1-2	s, cd,	1040	2490	90	25	<i>Thalassodendron</i> - <i>Halimeda</i>	1.73
N-E	13	1	s, cd,	1396	3257	100	25	<i>Thalassodendron</i> - <i>Halimeda</i>	0.68
W	14	8	s, cd,	1564	3570	50	30	<i>Thalassodendron</i> - <i>Caulerpa</i>	1.00
W	15	1.5	s, cd	-	1300	-	10	<i>Halimeda</i>	0.12
W	16	2.5	s, cd	-	429	-	10	<i>Halimeda</i>	0.15
W	17	3.5	s, cd	84	1690	-	20	(<i>Thalassodendron</i>)- <i>Halimeda</i>	0.36
W	18	3.5	s, cd	-	3400	-	10	<i>Halimeda</i>	0.12
W	19	4.0	s, cd	-	5078	-	10	<i>Halimeda</i>	0.05
W	20	4.5	s, cd	-	2628	-	10	<i>Halimeda</i>	0.15
W	21	3.0	s, cd	1060	3144	-	21	<i>Thalassodendron ciliatum</i>	0.38
W	22	4.5	s, cd	336	1474	-	22	<i>Thalassodendron</i> - <i>Halimeda</i>	1.38
W	23	5-6	s, cd	188	1026	-	25	<i>Thalassodendron</i>	0
E	24	mih	s, cd	668	362	80	12	<i>Thalassia</i>	0
E	25	mih	s, cd	1516	1820	100	25	<i>Thalassodendron</i> - <i>Thalassia</i>	0.25
E	26	lih	s, cd	2532	2930	100	25	<i>Thalassodendron</i> - <i>Dictyurus</i>	0.45
E	27	2	s, cd	1416	2645	100	20	<i>Thalassodendron</i> - <i>Halimeda</i> - <i>Dictyurus</i>	0.76
E	28	7	s, cd	792	1533	80	20	<i>Thalassodendron</i> - <i>Halimeda</i>	0.39
E	29	25	s, cd	28	583	30	12	(<i>Thalassodendron</i>)- <i>Caulerpa</i> - <i>Halimeda</i>	1.60
N-E	30	3.0	s, cd	788	1700	100	18	(<i>Thalassodendron</i>)- <i>Caulerpa</i> - - <i>Halimeda</i>	0.70
N-E	31	6	s, cd	-	1221	95	10	<i>Halimeda</i> + <i>Boodlea</i> + <i>Microdictyon</i>	2.47
N-E	32	7	s, cd	74C	1809	50	23	<i>Thalassodendron</i> - <i>Halimeda</i>	0.42
N-E	33	17	s, cd	468	1640	-	-	<i>Thalassodendron</i> - <i>Halimeda</i>	0.42
N-E	34	25	s, cd	832	2319	10	27	<i>Thalassodendron</i> - <i>Halimeda</i>	0.21

Table 2. Continued.

Coast	Station	Depth in m, zone	Substrate	# of species·m ⁻²	Biomass, in g·m ⁻²	% cover	Growth height	Association	H
N-E	35	mih	s, cd	1096	1061	80	15	<i>Thalassia</i>	0
N-E	36	mih	s, cd	492	2501	100	16	<i>Thalassodendron</i> + <i>Thalassia</i>	0.67
N-E	37	lih	s, cd	3004	3360	100	17	<i>Thalassodendron</i> - <i>Dictyurus</i>	0.37
N-E	38	32	s, cd	-	-	15	25	<i>Avrainvillea</i> - <i>Halimeda</i>	-
S	39	5	s, cd	868	2087	50	20	<i>Thalassodendron</i>	0.62
S	40	10	s, cd	684	1164	40	21	<i>Thalassodendron</i>	0.33
S	41	12	s, cd	28	418	40	18	(<i>Thalassodendron</i>)- <i>Halimeda</i> - <i>Microdictyon</i>	1.55
W	42	mih	f, s	1840	1401	100	23	<i>Thalassia</i> + <i>Halodule</i>	2.46
W	43	mih	f, s	3240	5051	100	40	<i>Syringodium</i> + <i>Thalassodendron</i>	1.24
W	44	mih	f, s	3336	2592	100	30	<i>Halodule</i> + <i>Thalassia</i>	1.73
W	45	lih	cd	1960	3994	100	20	<i>Thalassodendron</i>	0
W	46	3	s, c	732	2040	40	24	<i>Thalassodendron</i>	0.44
W	47	3	s, c	692	1736	40	25	<i>Thalassodendron</i>	0
W	48	6	s, c	1088	2467	30	27	<i>Thalassodendron</i>	0
W	49	7	s, cb	376	668	20	24	<i>Thalassodendron</i>	0
W	50	17	s, cb	120	681	20	21	<i>Thalassodendron</i> - <i>Dictyurus</i>	1.12
W	51	1.5	s	1080	2322	100	18	<i>Thalassodendron</i>	0
Farquhar Island									
S	52	mih	s	732	541	40	15	<i>Thalassodendron</i> + <i>Thalassia</i>	0.45
S	53	lih	s, cd	888	897	70	13	<i>Thalassodendron</i>	0.12
S	54	lih	s, cd	-	1660	60	1-2	<i>Boodlea</i>	0
S	55	lih	s, cd	128	720	80	15	(<i>Thalassodendron</i>)- <i>Caulerpa</i> - <i>Boodlea</i>	2.26
S	56	6	s, cd	-	261	5	3	<i>Caulerpa</i>	0.08
S	57	15	s, cd	-	266	50	1-2	<i>Microdictyon</i> + <i>Boodlea</i>	0.18
S	58	25	s, cd	-	180	60	1-2	<i>Microdictyon</i>	0
N	59	mih	b, r	1068	1014	5	8	<i>Thalassodendron</i> - <i>Boodlea</i>	0.85
N	60	lih	s, cd	-	1360	80	1-2	<i>Boodlea struveoides</i>	0
N	61	lih	s, cd	-	1273	50	1-2	<i>Microdictyon</i> + <i>Boodlea</i>	1.24
N-E	62	6-7	s, cd	-	354	5	2	<i>Caulerpa</i> + <i>Boodlea</i>	0.24
N-E	63	12h	d, c	-	130	20	2	<i>Caulerpa</i>	0
N-E	64	22	d, c	-	340	20	2-5	<i>Udotea</i> + <i>Caulerpa</i>	0.52
Lagoon	65	3	d, c	-	520	1	2	<i>Caulerpa cupressoides</i>	0
Lagoon	66	7	d, cd	-	440	3	2	<i>Caulerpa cupressoides</i>	0
Lagoon	67	9	d, cd	-	236	5-7	2	<i>Halimeda opuntia</i> + <i>Caulerpa cupressoides</i>	0.95
Lagoon	68	2.5	s, cd	472	1289	80	28	<i>Thalassodendron</i>	0.10
Lagoon	69	8	s	-	-	0	-	-	-
Lagoon	70	12	s	-	-	0	-	-	-
Lagoon	71	3	s, cd	918	4563	90	35	<i>Thalassodendron</i> - <i>Halimeda</i>	0.90
Lagoon	72	1.2	s, cd	664	2652	100	24	<i>Thalassodendron</i> - <i>Halimeda</i>	1.11
Lagoon	73	1.0	s, cd	1004	2614	100	28	<i>Thalassodendron</i> - <i>Caulerpa</i>	0.20

Table 2. Continued.

Coast	Station	Depth in m, zone	Substrate	# of species-m ⁻²	Biomass, in g-m ⁻²	% cover	Growth height	Association	H
Lagoon	74	8	s, cd	-	-	0	-	-	-
Lagoon	75	10	s, c	-	-	0	-	-	-
Lagoon	76	12	l, c	-	-	0	-	-	-
Lagoon	77	6	s, c	-	-	1	-	<i>Heterosiphonia</i>	-
Lagoon	78	3-4	s, cd	446	2258	100	30	<i>Thalassodendron-Halimeda</i>	0.93
Lagoon	79	2	s, cd	868	2736	100	126	<i>Thalassodendron-Thalassia</i>	0.23
Lagoon	80	1	s, cd	848	1446	100	20	<i>Thalassodendron-Caulerpa</i>	0.54
N	81	mih	s, cd	584	1210	100	14	<i>Thalassodendron-Caulerpa</i>	1.49
N	82	lih	s, cd	1352	1850	100	12	<i>Thalassodendron-Valonia</i> + <i>Microdictyon</i>	1.05
N	83	lih	s, cd	1160	1567	100	12	<i>Thalassodendron-Valonia</i>	0.88
N	84	4	cd	120	2880	100	50	<i>Sargassum ilicifolium</i>	0
S	85	1	cd	-	-	70	25	<i>Thalassodendron</i>	-
Aldabra Island									
E	86	12	s, cd	-	2828	60	10	<i>Halimeda</i>	0
E	87	25	s, cd	-	451	20	10	<i>Halimeda</i>	0
E	88	12	Halimeda s	-	-	-	30	10 <i>Halimeda</i>	-
Lagoon	89	lih	s, cd	518	1259	70	18	(<i>Thalassodendron</i>)- <i>Laurencia</i> + <i>Halimeda</i>	1.87
Lagoon	90	lih	s, cd	376	579	70	12	<i>Thalassia</i> + <i>Laurencia</i>	0.70
Lagoon	91	lih	s, cd	284	5467	80	25	<i>Thalassia</i> + <i>Halimeda</i>	1.24
Lagoon	92	mih	s, cd	584	1465	80	17	<i>Thalassia</i> + <i>Halimeda</i>	1.44
Lagoon	93	5	s, cd	960	2050	100	24	<i>Thalassia</i>	0.32
W	94	1	s, black c	1004	2718	100	24	<i>Thalassodendron</i>	0.19
W	95	lih	s, black c	960	1970	100	15	<i>Thalassodendron</i> + <i>Thalassia</i> - <i>Halimeda</i>	1.49
W	96	lih	s, black c	768	2089	100	17	<i>Thalassodendron</i> + <i>Thalassia</i> - <i>Halimeda</i>	1.20
W	97	lih	s, black c	-	-	100	20	<i>Thalassodendron</i> + <i>Halimeda</i>	-
Desroches Island									
N-W	98	mih	s	788	662	80	20	<i>Thalassodendron</i> + <i>Thalassia</i> - <i>Halimeda</i>	
N-W	99	mih	s, cd	1476	2400	100	30	<i>Thalassodendron-Halimeda</i> - <i>Haloplegma</i>	1.20
N-W	100	lih	s, cd	1456	3864	100	42	<i>Thalassodendron</i>	0.12
N-W	101	2	s, cd	-	-	70	40	<i>Thalassodendron</i>	-
N-W	102	6	s, cd	648	2164	100	42	<i>Thalassodendron</i>	0
N-W	103	12	s, cd	408	1572	50	25	<i>Thalassodendron-Halimeda</i> + <i>Udotea</i>	1.43
N-W	104	4-5	s, cd	-	1700	25	10	<i>Halimeda</i>	0

Table 2. Continued.

Coast	Station	Depth in m, zone	Substrate	# of species·m ⁻²	Biomass, in g·m ⁻²	% cover	Growth height	Association	H
N-W	105	30	s, cd	-	-	5	20	<i>Thalassodendron-Halimeda</i>	-
N-W	106	mih	s	1526	1420	80	20	<i>Thalassia + Thalassodendron</i> <i>-Halimeda</i>	1.34
N-W	107	mih	s	1324	2471	100	20	<i>Thalassia + Thalassodendron</i> <i>-Halimeda</i>	1.60
N-W	108	lih	s, cd	1232	4441	100	30	<i>Thalassodendron-Thalassia-Halimeda</i>	
N-W	109	lih	s, cd	2600	5095	100	40	<i>Thalassodendron</i>	
S-E	110	13	cd	-	-	40	40	<i>Thalassodendron-Halimeda</i>	-
S-E	111	30	Hs	-	-	5	10	<i>Halimeda</i>	-
W	112	2	s, cd	1282	4126	90	38	<i>Thalassodendron</i>	0
W	113	7	c	-	1185	50	10	<i>Halimeda</i>	0
W	114	8	c	1468	3768	50	40	<i>Thalassodendron</i>	0
W	115	12	s, c	-	-	15	10	<i>Halimeda</i>	-
S	116	mih	s	1396	596	100	6	<i>Thalassia + Thalassodendron</i> <i>-Udotea</i>	1.30
S	117	mih	s	1432	563	100	6	<i>Thalassodendron-Thalassia-Udotea</i>	1.62
S	118	lih	s, cd	1672	1146	70	15	<i>Thalassodendron-Thalassia</i>	1.24
S	119	lih	cd	1732	2244	70	25	<i>Thalassodendron-Halimeda</i> <i>+Dictyurus</i>	1.57
S	120	5-6	cd	1780	3269	60	33	<i>Thalassodendron</i>	0
S	121	20	s	4	929	30	10	<i>Halimeda</i>	0
S	122	35-38	s	-	-	10	10	<i>Halimeda</i>	0
S-E	123	50	s, cd	-	-	1	10	<i>Halimeda</i>	-
S-E	124	1.5-3	cd	764	2016	50	30	<i>Thalassodendron</i>	0.23
S-E	125	6	cd	1192	2048	40	30	<i>Thalassodendron</i>	0.14
S-E	126	15	cd	-	40	10		<i>Halimeda</i>	0.13
S-E	127	16-30	s	-	888	5	10	<i>Halimeda</i>	0
S-E	128	42	s	-	-	1	5	<i>Caulerpa + Halimeda</i>	-
S-E	129	30	s	-	-	1	10	<i>Caulerpa + Halimeda</i>	-
S-E	130	13	s	-	-	1	30	<i>Thalassodendron-Halimeda</i>	-
S-E	131	20	s	-	-	1	10	<i>Halimeda</i>	-
S-E	132	50	s	-	-	1	10	<i>Halimeda + Caulerpa</i>	-
S	133	mih	s	2312	2222	100	20	<i>Cymodocea + Thalassodendron</i> <i>+Syringodium</i>	1.33
S	134	lih	s, cd	1776	4260	100	30	<i>Thalassodendron</i>	0
S	135	lih	s, cd	2184	4100	100	40	<i>Thalassodendron</i>	0
S	136	1.2	cd	1244	9800	100	60	<i>Sargassum</i>	0
S	137	1.5-3	cd	516	6800	90	60	<i>Sargassum</i>	0.16
S	138	9	cd	8	621	10	40	<i>Sargassum</i>	0.21
S	139	20	cd	-	-	1	3	<i>Hypnea, Laurencia</i>	-
S-W	140	mih	s	784	1250	80	16	<i>Syringodium + Cymodocea</i> <i>+Thalassia</i>	1.20
S-W	141	lih	s	2448	2898	100	30	<i>Syringodium + Cymodocea</i>	0.30
S-W	142	lih	s	1356	2153	100	30	<i>Cymodocea-Syringodium</i>	0.76
S-W	143	lih	s, cd	1112	3776	40	50	<i>Sargassum cristaefolium-Padina</i> sp.	0.80
S-W	144	0.5	s, cd	656	5858	80	60	<i>Sargassum -Turbinaria</i>	
S-E	145	5	s, cd	248	1010	40	40	<i>Sargassum</i>	0

Table 2. Continued.

Coast	Station	Depth in m, zone	Substrate	# of species·m ⁻²	Biomass, in g·m ⁻²	% cover	Growth height	Association	H
S-E	146	17	s	-	-	1	30	<i>Thalassodendron-Dictyota</i>	-
S-E	147	20	s	-	-	0.5	-	<i>Chlorodesmis</i>	-
S-E	148	5	cd	128	1480	50	50	<i>Sargassum</i>	0
S-E	149	8	cd	96	840	60	60	<i>Sargassum</i>	0
S-E	150	8	cd	-	-	5	-	<i>Chlorodesmis</i>	-
Mahé (Cerf)									
W	151	lih	s, cd	948	4465	80	20	<i>Sargassum</i>	0.10
W	152	lih	s, cd	332	5700	100	30	<i>Sargassum-Jania+Gelidiella</i>	-
W	153	0.5	cd	376	5600	100	30	<i>Sargassum</i>	0
W	154	mih	s	111	1396	70	10	<i>Cymodocea</i>	0
Mahé (Saint Anne) Island									
E	155	mih	s	600	3304	70	30	<i>Sargassum poslycystum</i> <i>Turbinaria ornata</i>	0.78
E	156	lih	s, cd	708	6500	100	20	<i>Sargassum cristaefolium</i>	0
E	157	0.5	cd	268	5292	100	30	<i>Sargassum-Turbinaria</i>	0.55
E	158	mih	rock	8	2935	40	20	<i>Garcilaria crassa</i>	0.22
E	159	mih	silty s	624	342	40	10	<i>Cymodocea+Halodule</i>	0.75
Mahé Island									
N-E	160	mih	s, cd	236	6426	80	30	(<i>Sargassum</i>)- <i>Gracilaria</i>	1.10
N-E	161	mih	s, cd	204	6619	90	30	(<i>Sargassum</i>)- <i>Gracilaria</i>	-
N-E	162	lih	s, cd	216	5216	100	30	<i>Sargassum</i>	1.49
N-E	163	lih	s, cd	328	4240	100	30	<i>Sargassum</i>	0
N-E	164	3-6	cd	-	1400	30	10	<i>Turbinaria decurrens</i>	0
N-E	165	15-16	cd	-	-	-	-	<i>Chlorodesmis</i>	-
N-E	166	3-7	cd	-	-	30	40	<i>Sargassum</i>	-
N-E	167	13-14	cd	28	2016	20	30	<i>Sargassum</i>	0.39
Anonyme Island									
N-E	168	0.5	rock	720	7480	80	30	<i>Sargassum</i>	0
N-E	169	0.5	cd	456	6340	100	40	<i>Sargassum</i>	0
N-E	170	0.5	cd	517	6933	100	20	<i>Sargassum</i>	0
N-E	171	0.5	cd	152	3320	100	20	<i>Sargassum</i>	0
N-E	172	0.2	cd	112	2900	100	20	<i>Sargassum</i>	0
N-E	173	2-11	cd	-	-	0	-	crustose algae	-
N-E	174	15	cd	-	-	1	-	<i>Lobophora+Dasya</i>	-
N-E	175	22	cd	-	-	-	-	-	-

Table 2. Continued.

Coast	Station	Depth in m, zone	Substrate	# of species·m ⁻²	Biomass, in g·m ⁻²	% cover	Growth height	Association	H
Mahé Island									
S-E	176	0.4	s, cd	284	1816	60	30	<i>Sargassum-Amphiroa-Caulerpa</i>	-
S-E	177	0.5	s, cd	500	2965	60	30	<i>Sargassum</i>	0.42
S-E	178	0.5	s, cd	116	5471	70	30	<i>Sargassum-Amphiroa</i>	0.84
S-E	179	0.5	s, cd	525	3986	90	15	<i>Sargassum</i>	0.11
N-W	180	lih	s, cd	992	1675	60	20	<i>Thalassodendron-Hypnea</i>	1.50
N-W	181	lih	s, cd	500	2503	70	18	<i>Turbinaria ornata-Hypnea pannosa</i>	1.10
N-W	182	lih	s, cd	316	3638	100	30	<i>Sargassum turbinarioides-Hypnea</i>	0.27
N-E	183	31	s	-	-	-	single	<i>Champia parvula</i>	-
N-E	184	22	s, rock	-	-	-	single	<i>Dictyota bartayresii+Hypnea</i>	-
S-E	185	30	s	-	-	-	-	<i>Dictyota+Gracilaria cylindrica</i>	-
S-E	186	10-15	cd	-	-	-	-	crustose algae	-
African Banks									
S-E	187	15	cd	324	1206	50	32	<i>Thalassodendron</i>	0
S-E	188	10	cd	248	440	80	30	<i>Thalassodendron</i>	0.29
S-E	189	1.5	cd	540	1400	90	27	<i>Thalassodendron</i>	0.31
S-E	189a	6-7	cd	570	2215	80	26	<i>Thalassodendron</i>	0.15
S-E	190	17	cd	-	-	-	-	<i>Thalassodendron</i>	-
S-E	191	25	cd	-	-	-	-	<i>Thalassodendron</i>	-
S-E	192	18	cd	-	-	-	-	<i>Thalassodendron</i>	-
S-E	193	31	cd	-	-	-	-	<i>Thalassodendron</i>	-
S-E	194	17-19	cd	448	2240	50	42	<i>Thalassodendron</i>	0
S-E	195	0.6	s, cd	1412	2517	100	18	<i>Thalassodendron</i>	0
S-E	196	0.5	s, cd	716	2057	100	20	<i>Thalassodendron-Valonia-Thalassia</i>	1.63
S-E	197	0.5	s, cd	1096	2125	100	25	<i>Thalassodendron-Thalassia</i> <i>-Microdictyon</i>	1.50
S-E	198	0.5	s, cd	1268	2602	100	25	<i>Thalassodendron</i>	0.12
N-W	199	1.5	s	-	330	15	8	<i>Dasya+Halimeda</i>	0.90
S-E	200	37	s	-	-	-	-	<i>Halimeda</i>	-
Saint Joseph Islands (D'Arros, Ressource)									
S	201	mih	s, cd	-	1003	50	10	<i>Thalassia hemprichii</i>	0
S	202	mih	s, cd	1312	1018	50	11	<i>Thalassodendron-Thalassia</i> <i>-Dictyosphaeria</i>	1.22
S	203	lih	cd	608	430	50	10	<i>Thalassodendron-Thalassia</i>	0.94
S	204	lih	cd	-	1150	30	-	<i>Cladophoropsis+Valonia</i>	0.66
S	205	30	cd	-	-	-	-	-	-
S	206	16	cd	-	-	-	-	-	-
S	207	3-5	cd	-	-	1-5	-	<i>Halimeda</i>	-
S	208	1	cd	-	-	20	-	<i>Thalassodendron</i>	-

Table 2. Continued.

Coast	Station	Depth in m, zone	Substrate	# of species·m ⁻²	Biomass, in g·m ⁻²	% cover	Growth height	Association	H
S	209	37	cd	-	-	-	-	<i>Halimeda</i>	-
S	210	23	cd	-	-	-	-	<i>Halimeda</i>	-
S	211	37	cd	-	-	-	-	<i>Halimeda</i>	-
S	212	0.5	s	1264	1637	80	30	<i>Thalassodendron</i>	-
S	213	lih	s	1148	1005	50	20	<i>Thalassodendron-Microdictyon</i>	1.14
S	214	lih	s	1416	2265	80	30	<i>Thalassodendron</i>	0.79
S	215	0.3	s	1384	2956	60	30	<i>Thalassodendron</i>	0.26
S	216	25	c	-	-	1	-	Crustose algae	-
S	217	18	c	-	-	1	-	<i>Halimeda</i>	-
S	218	7-8	c	-	-	5	-	<i>Halimeda</i>	-
E	219	10-12	c	6	-	5	-	<i>Thalassodendron-Udotea</i>	-
N-E	220	1-1.5	cd	740	1680	50	40	<i>Thalassodendron</i>	0
N-E	221	5-6	cd	-	-	10	10	<i>Halimeda</i>	-
S	222	20	s, c	-	-	-	-	<i>Boodlea struveoides</i>	-
S	223	30	s, c	-	-	-	-	<i>Halimeda + Caulerpa</i>	-
Providence Atoll									
S	224	1.5	cd	924	3940	100	30	<i>Thalassodendron</i>	0
S	225	13	cd	784	2302	90	30	<i>Thalassodendron</i>	0.11
S	226	23	cd	2876	3911	30	30	<i>Thalassodendron</i>	0.27
W	227	1.5	cd	-	-	80	30	<i>Thalassodendron-Microdictyon</i>	-
W	228	23	cd	-	-	30	20	<i>Thalassodendron-Microdictyon</i>	-
S-W	229	32	cd	-	-	-	-	<i>Halimeda</i>	-
S-W	230	3-6	cd	-	-	-	-	<i>Thalassodendron</i>	-
Cosmoledo Islands									
Lagoon	231	0.4	s	392	1439	100	20	<i>Thalassodendron-Halimeda</i> <i>+Laurencia</i>	1.79
Lagoon	232	0.4	s	916	2616	100	25	<i>Thalassodendron-Halimeda</i>	1.07
Lagoon	233	0.4	s	716	5547	100	35	<i>Thalassodendron-Halimeda</i>	1.01
Lagoon	234	0.4	s	688	1995	100	30	<i>Thalassodendron-Laurencia</i>	1.10
Lagoon	235	0.2	s	172	280	80	10	<i>Thalassia + Cymodocea-Jania</i>	1.67
Lagoon	236	0.1	s	2592	192	60	6	<i>Halodule uniervis</i>	0
E	237	4-5	cd	-	-	-	-	<i>Laurencia-Caulerpa</i>	-
E	238	10	cd	-	-	-	-	<i>Caulerpa</i>	-
E	239	20	cd	-	-	-	-	<i>Avrainvillea amadelpa-Halimeda</i>	-
N	240	mih	cd	-	-	20	-	<i>Caulerpa + Halimeda + Boodlea</i>	-
E	241	40	cd	-	-	-	-	<i>Halimeda + Microdictyon</i>	-
S	242	10	cd	-	-	-	-	<i>Turbinaria + Galaxaura + Halimeda</i>	-
E	243	42	cd	-	-	-	-	<i>Halimeda</i>	-
Lagoon	244	1.0	s, c	1644	3855	90	20	<i>Thalassodendron-Halimeda</i>	1.06
Lagoon	245	0.5	s, c	980	1513	60	20	<i>Thalassodendron-Halimeda</i>	0.50

Table 2. Continued.

Coast	Station	Depth in m, zone	Substrate	# of species·m ⁻²	Biomass, in g·m ⁻²	% cover	Growth height	Association	H
Astove Island									
S	246	lih	s	604	2558	100	25	(<i>Thalassia</i>)+ <i>Caulerpa</i> + <i>Amphiroa</i>	2.12
S	247	lih	s	1360	2422	100	30	<i>Thalassodendron-Laurencia</i> + <i>Thalassia</i>	2.53
S	248	lih	c	1540	1643	100	30	<i>Thalassodendron-Laurencia</i> + <i>Thalassia</i>	1.34
S	249	lih	c	2100	3227	100	20	<i>Thalassodendron-Laurencia</i>	1.46
Lagoon	250	0.3	s	-	-	20	15	<i>Thalassia-Caulerpa</i> + <i>Acanthophora</i>	-
S	251	1.5	c	1032	1380	40	8	<i>Halimeda</i> + <i>Caulerpa</i> sp.	-
S	252	5	c	-	-	20	8	<i>Halimeda</i> + <i>Caulerpa</i> sp.	-
S	253	30	c	-	1768	10	8	<i>Halimeda</i> + <i>Caulerpa</i> sp.	1.02
S-W	254	50	s, c	-	-	80	12	<i>Caulerpa</i> sp.+ <i>Halimeda copiosa</i>	-
S	255	50	s, c	-	-	60	12	<i>Caulerpa</i> sp.+ <i>Halimeda copiosa</i>	-
S	256	5-40	s, c	-	-	80-20	20	<i>Avrainvillea</i> + <i>Halimeda</i> + <i>Caulerpa</i> sp.	-

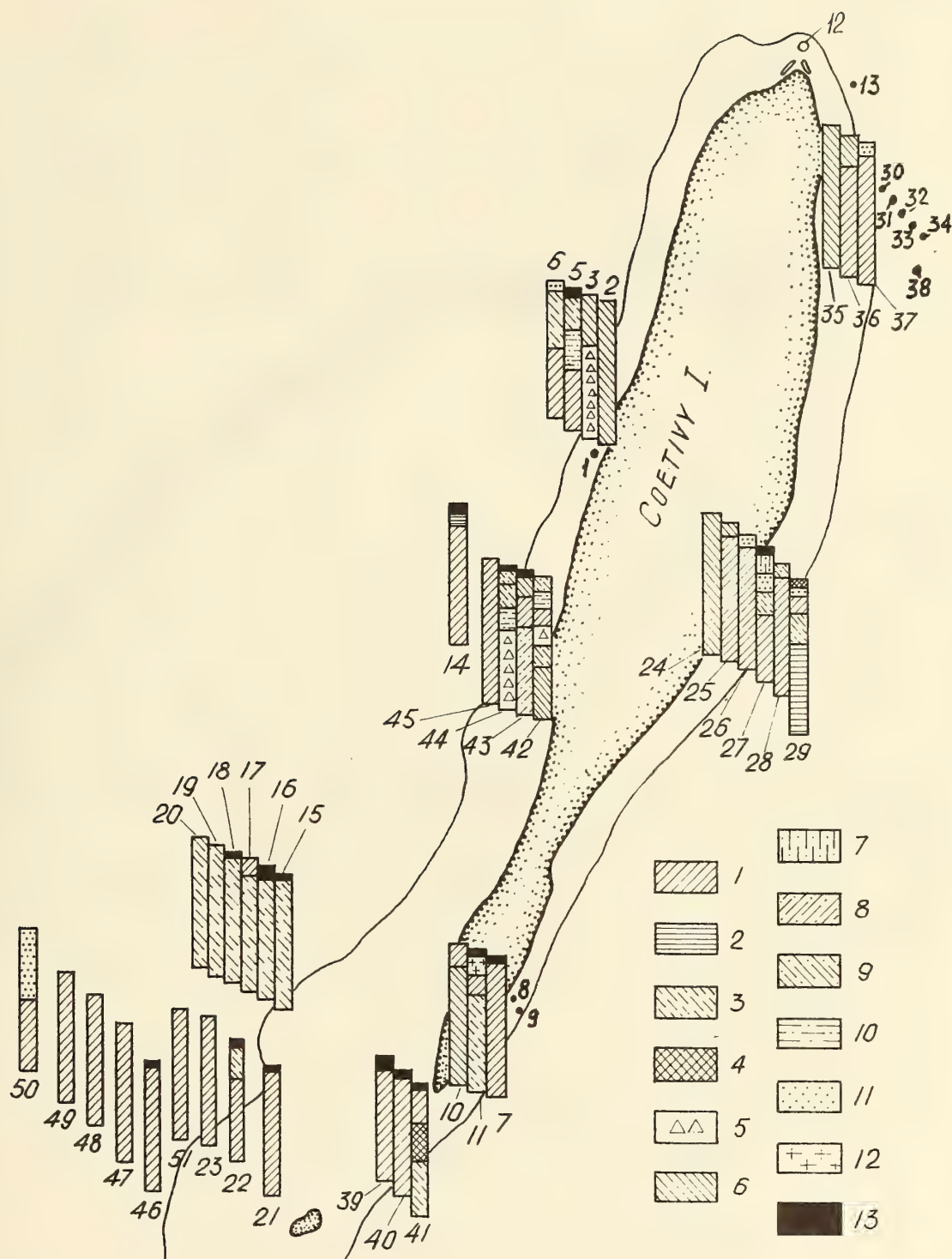


Figure 1. Location of stations and species ratios in phytocoenoses of Coetivy Island. 1 - *Thalassodendron ciliatum*, 2 - *Caulerpa cupressoides*, 3 - *Halimeda* species, 4 - *Microdictyon okamurai*, 5 - *Halodule uninervis*, 6 - *Thalassia hemprichii*, 7 - *Gelidiella myrioclada*, 8 - *Syringodium isoetifolium*, 9 - *Jania adhaerens*, 10 - *Hypnea pannosa*, 11 - *Dictyurus purpurascens*, 12 - *Laurencia* species, 13 - other minor species.

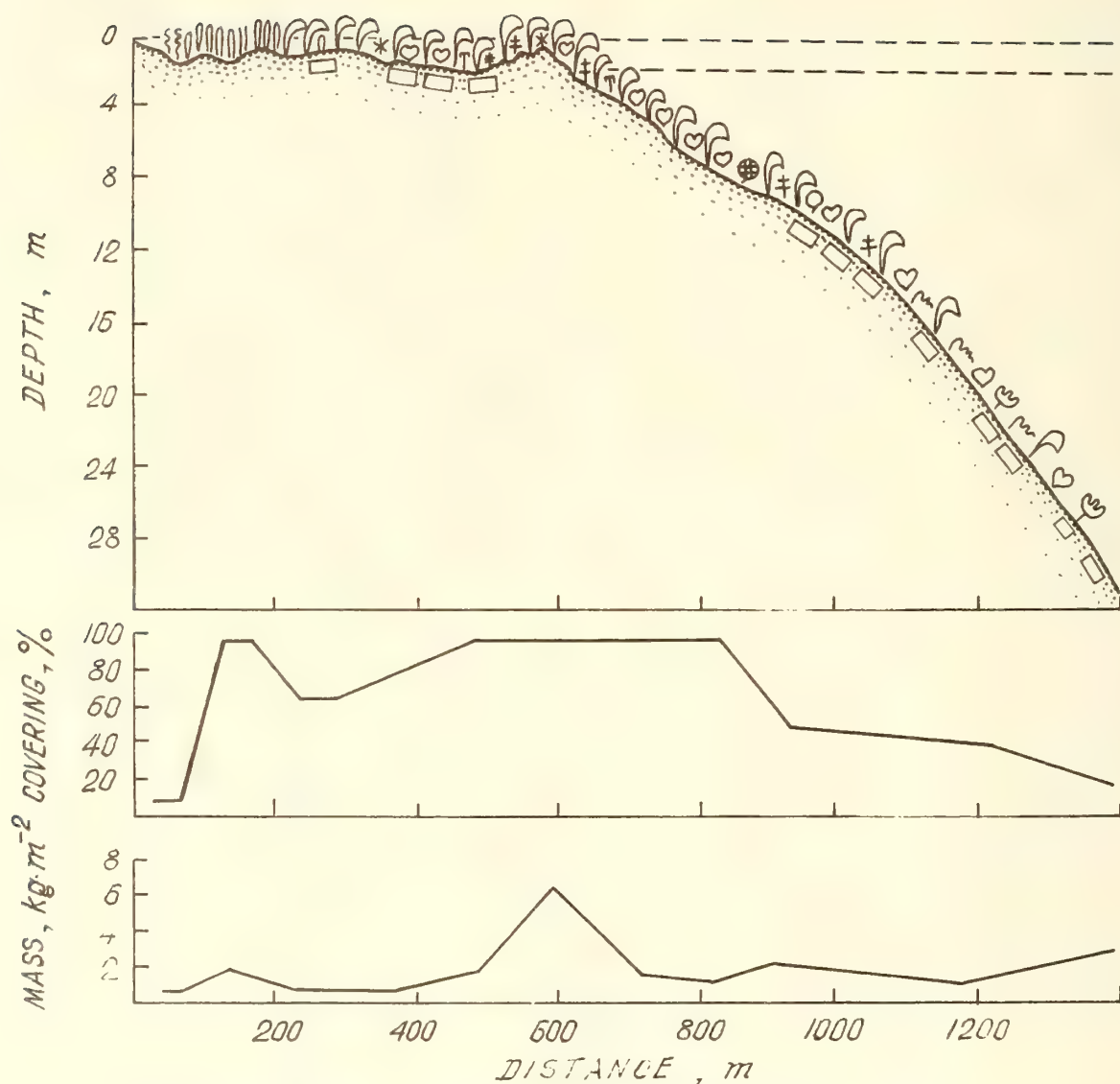


Figure 2. Vertical distribution of dominant species, biomass and percent cover of algae and seagrasses at Cöetivy Island. 1 - *Enteromorpha*, 2 - *Thalassia hemprichii*, 3 - *Halodule uninervis*, 4 - *Porolithon gardineri*, 5 - *Thalassodendron ciliatum*, 6 - *Laurencia* species, 7 - *Dictyurus purpurascens*, 8 - *Halimeda* species, 9 - *Caulerpa* species, 10 - *Avrainvillea amadelpha*, 11 - *Boodlea struveoides*.

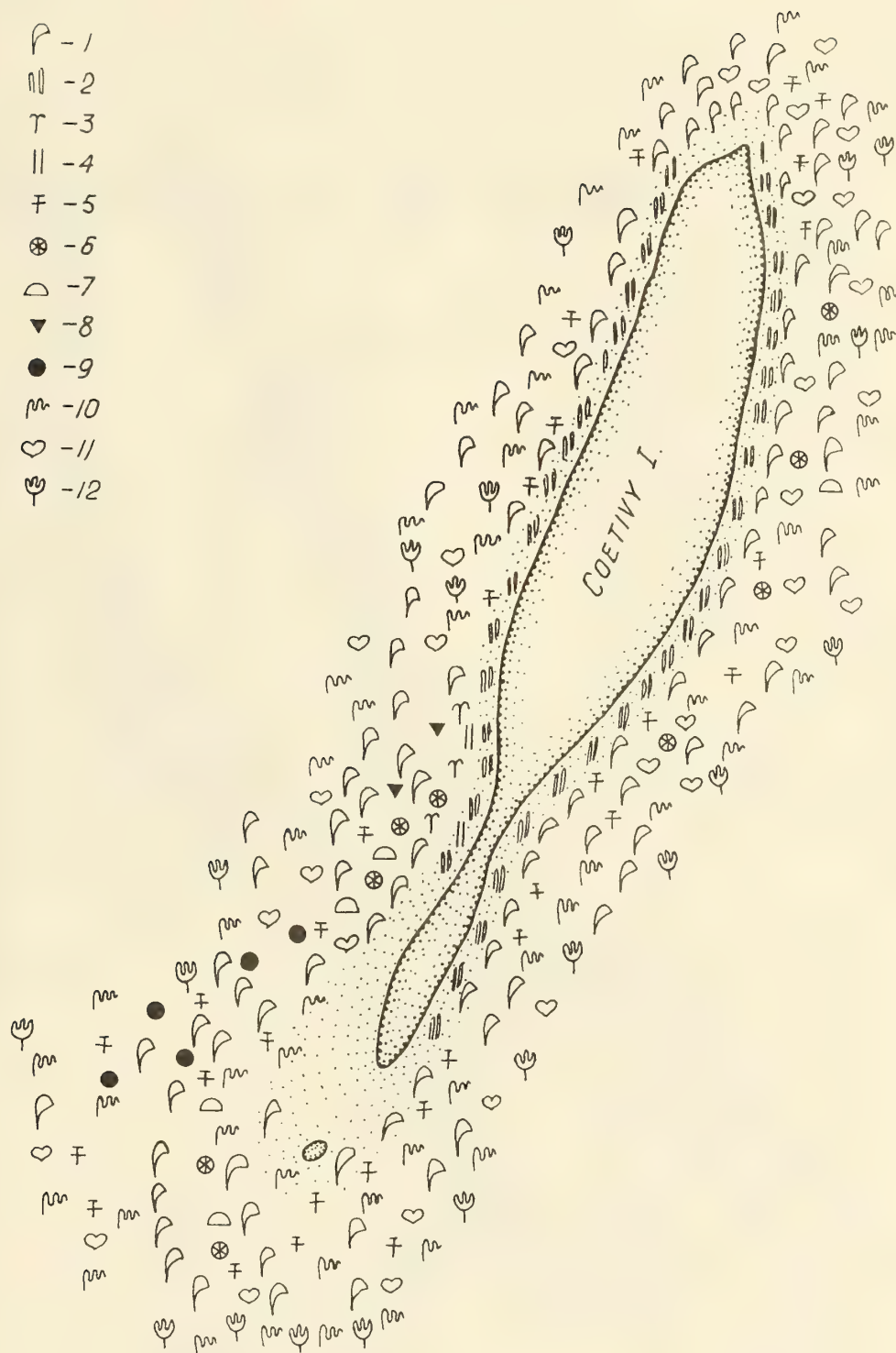


Figure 3. Horizontal distribution of algal and seagrass species of Cœtivy Island. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Syringodium isoetifolium*, 4 - *Halodule uninervis*, 5 - *Dictyurus purpurascens*, 6 - *Jania adhaerens*, 7 - crustose species, * - *Turbinaria ornata*, 9 - *Lobophora variegata*, 10 - *Caulerpa* species, 11 - *Halimeda* species, 12 - *Avrainvillea amadelpha* f. *submersa*.

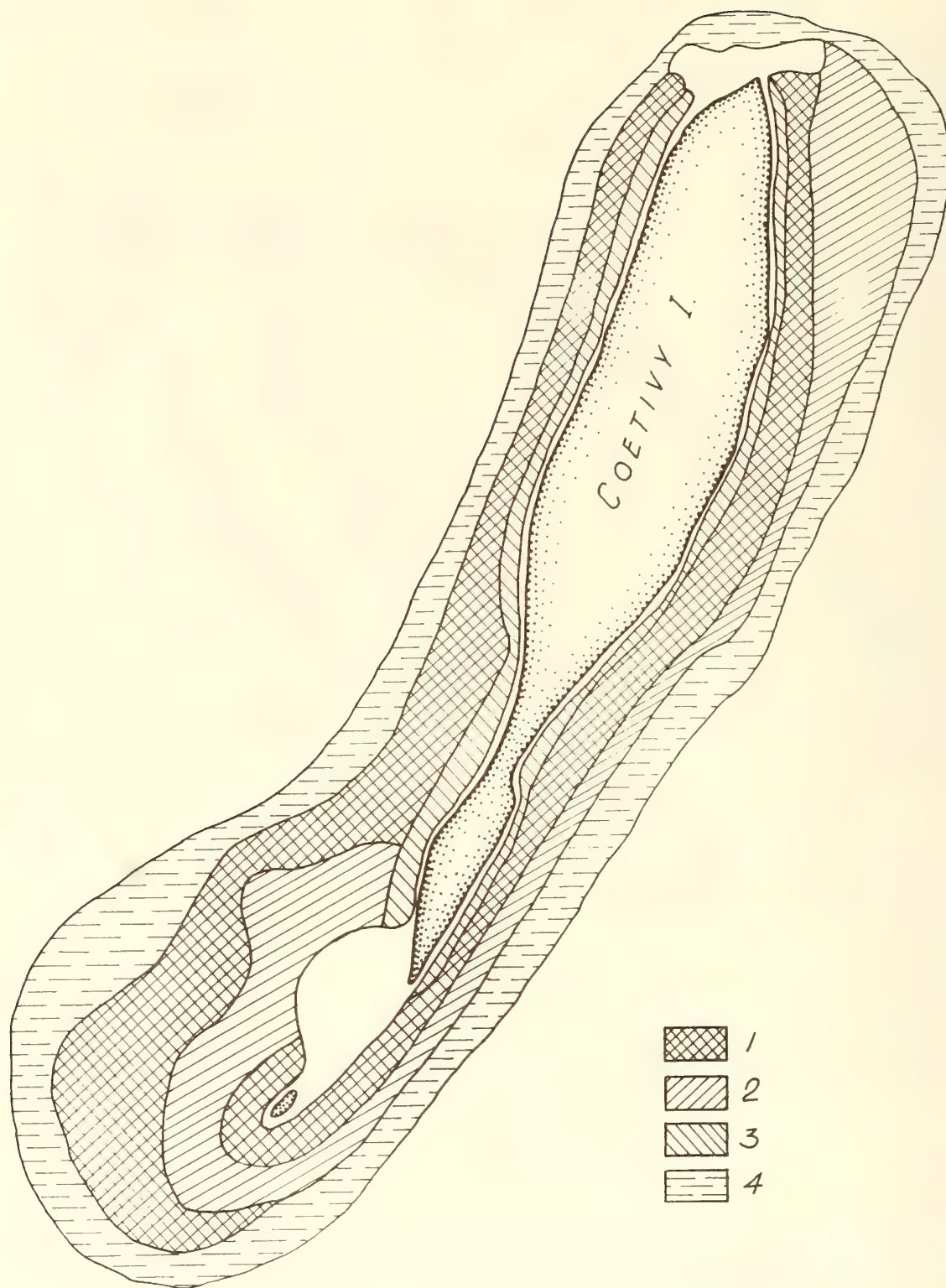


Figure 4. Distribution of macrophyte biomass at Cöetivy Island (in $\text{g}\cdot\text{m}^{-2}$): 1 - 3096 ± 393 ; 2 - 1597 ± 306 ; 3 - 878 ± 306 ; 4 - 557 ± 157 .

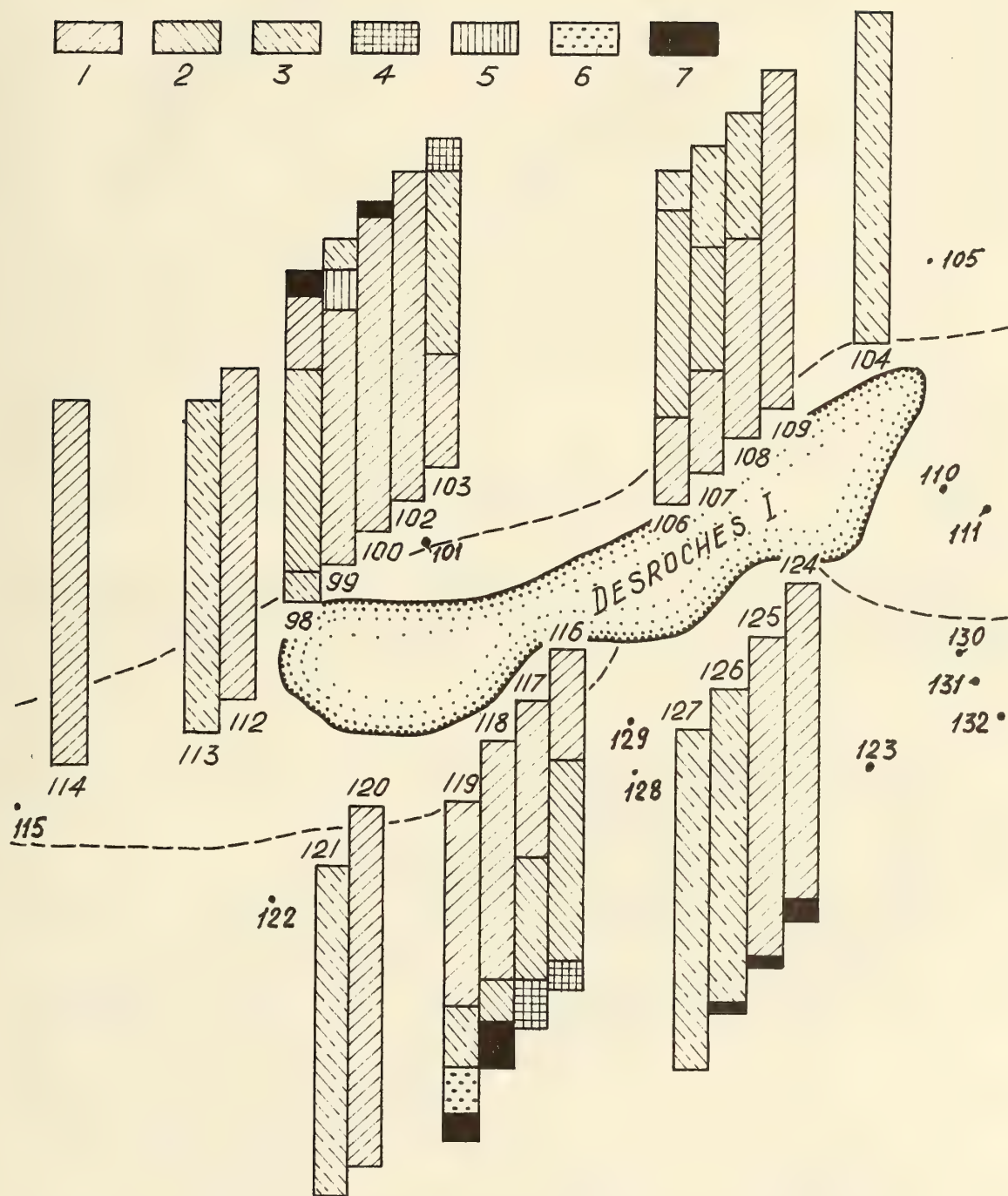
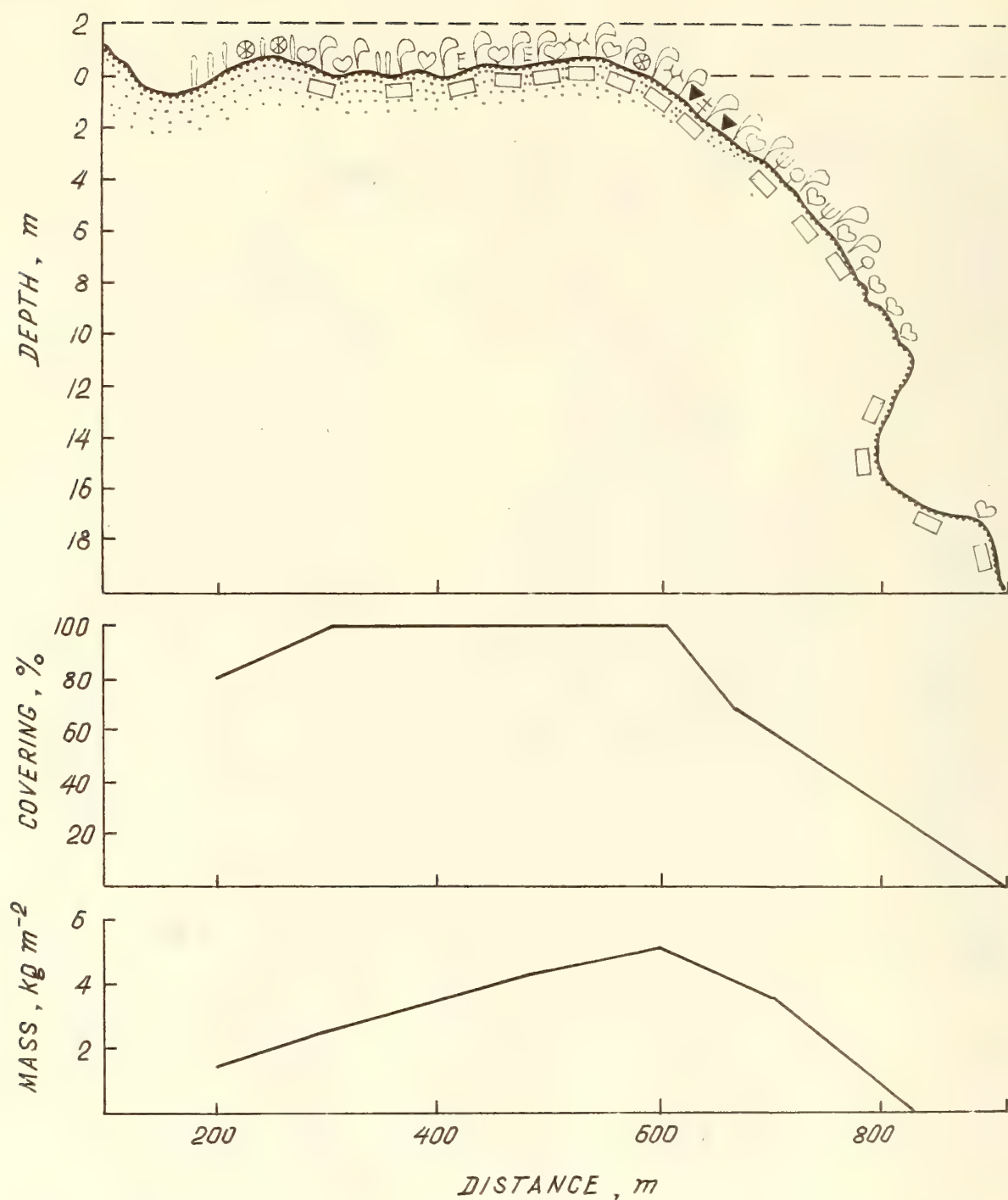


Figure 5. Location of stations and species ratios in phytocoenoses at Desroches Island. 1 - *Thalassia*, 3 - *Halimeda*, 4 - *Udotea*, 5 - *Haloplgema*, 6 - *Dictyurus*, 7 - other minor species.



⊖-1; ♀-2; ♥-3; ⊕-4; †-5; E-6; Ψ-7; ♀-8; ▼-9; ⚡-10

Figure 6. Vertical distribution of dominant species, biomass and percent cover of algae and seagrasses at Desroches Island. 1 - *Thalassia hemprichii*, 2 - *Thalassodendron ciliatum*, 3 - *Halimeda* species, 4 - *Jania adhaerens*, 5 - *Dictyurus purpurascens*, 6 - *Dasya mollis*, 7 - *Microdictyon okamurai*, 8 - *Rhipilia tomentosa*, 9 - *Turbinaria ornata*, 10 - *Tricleocarpa oblongata*.

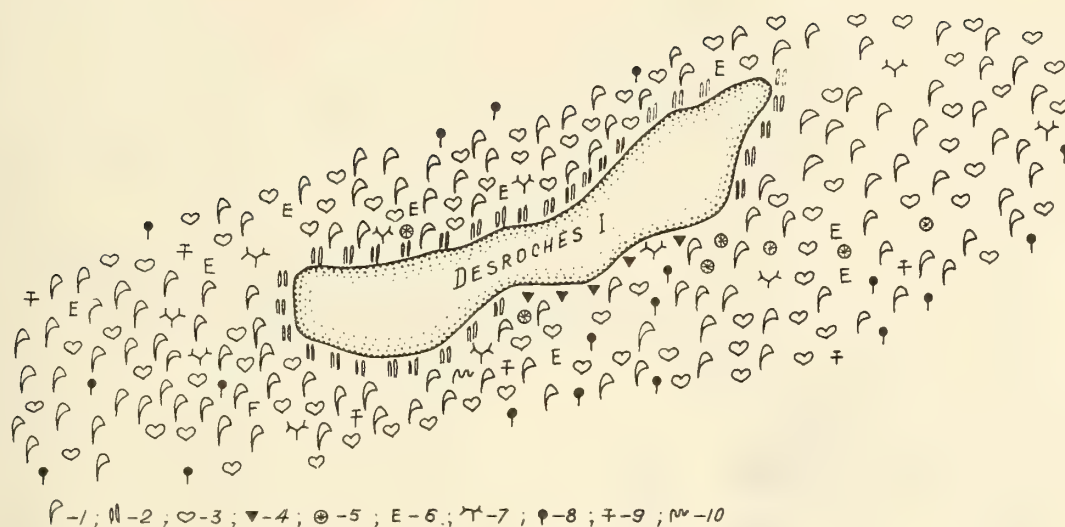


Figure 7. Horizontal distribution of algal and seagrass species at Desroches Island. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Halimeda*, 4 - *Turbinaria ornata*, 5 - *Jania* species, 6 - *Dasya mollis*, 7 - *Galaxaura* species, 8 - *Udotea argentea*, 9 - *Dictyurus purpurascens*, 10 - *Caulerpa* species.

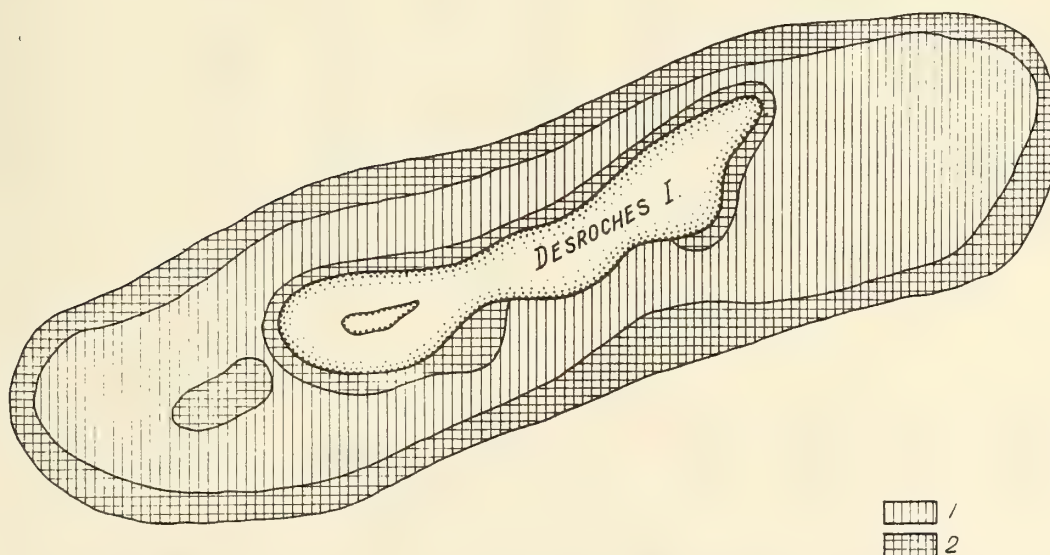


Figure 8. Distribution of macrophyte biomass at Desroches Island (in $\text{g}\cdot\text{m}^{-2}$): 1 - 3158 ± 680 ; 2 - 1241 ± 462 .

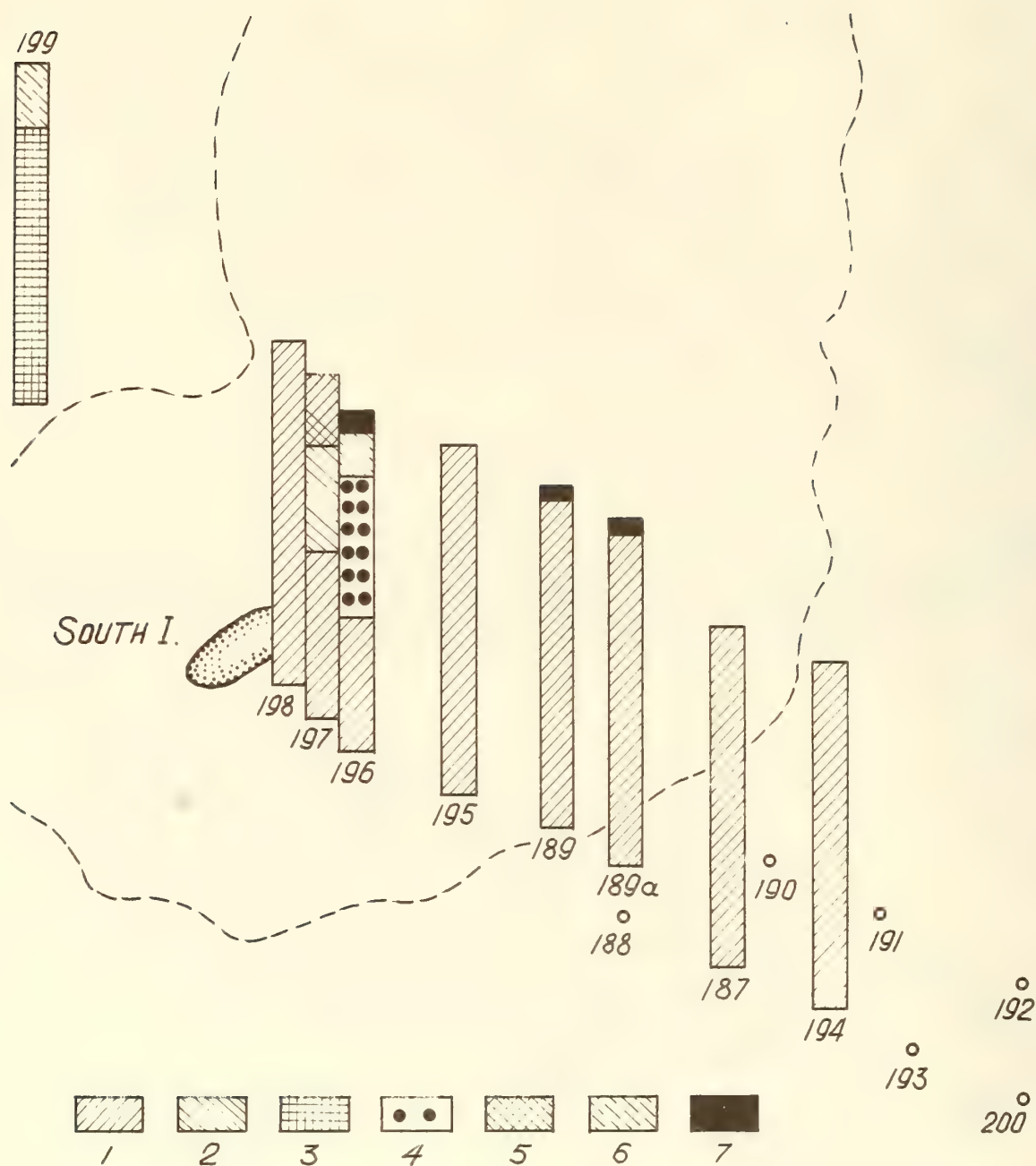


Figure 9. Location of stations and species ratios in phytocoenoses at African Banks (South Island).
 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Dasya mollis*, 4 - *Valonia fastigiata*, 5 - *Microdictyon okamurai*, 6 - *Halimeda* species, 7 - other minor species.

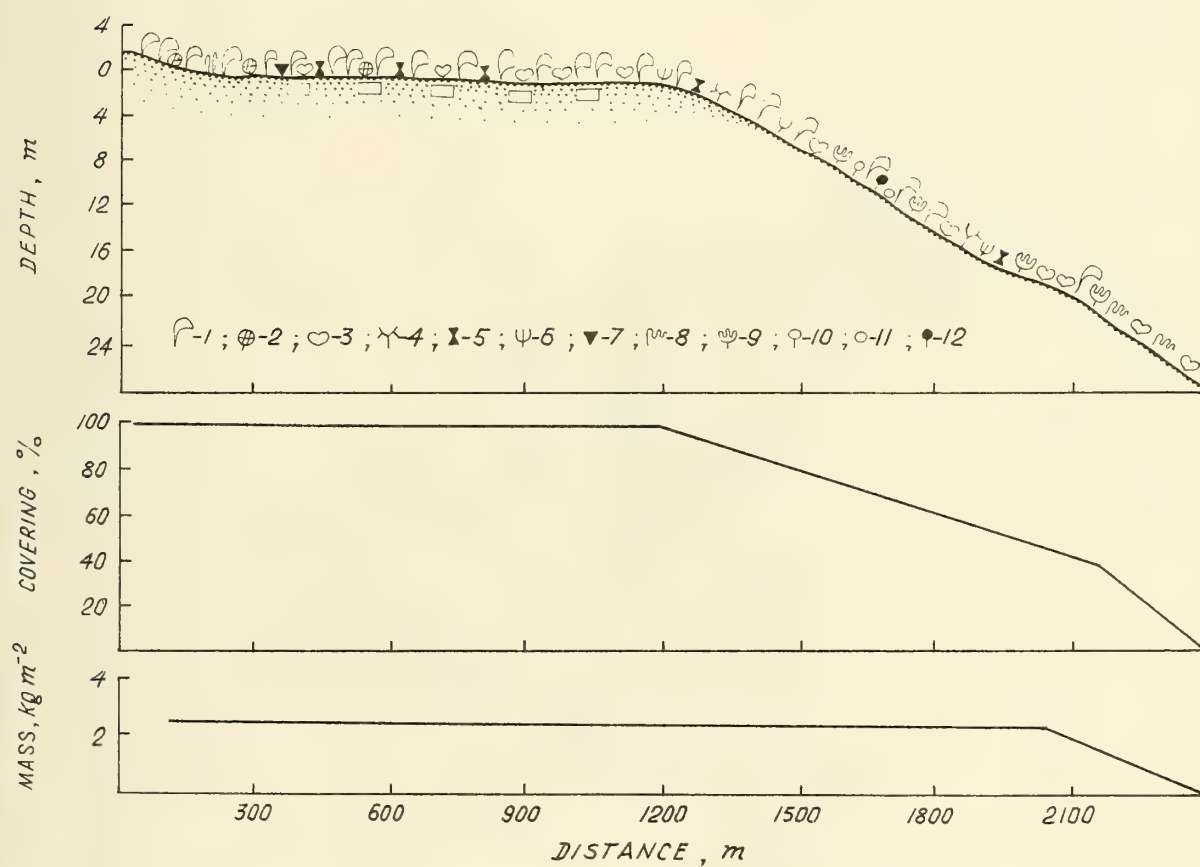


Figure 10. Vertical distribution of dominant species, biomass and percent cover of algae and seagrasses at African Banks. 1 - *Thalassodendron ciliatum*, 2 - *Boodlea struveoides*, 3 - *Halimeda* species, 4 - *Tricleocarpa oblongata*, 5 - *Haloplegma duperreyi*, 6 - *Microdictyon okamurai*, 7 - *Turbinaria oblongata*, 8 - *Caulerpa* species, 9 - *Avrainvillea amadelpha*, 10 - *Rhipilia tomentosa*, 11 - *Lobophora variegata*, 12 - *Udotea argentea*.

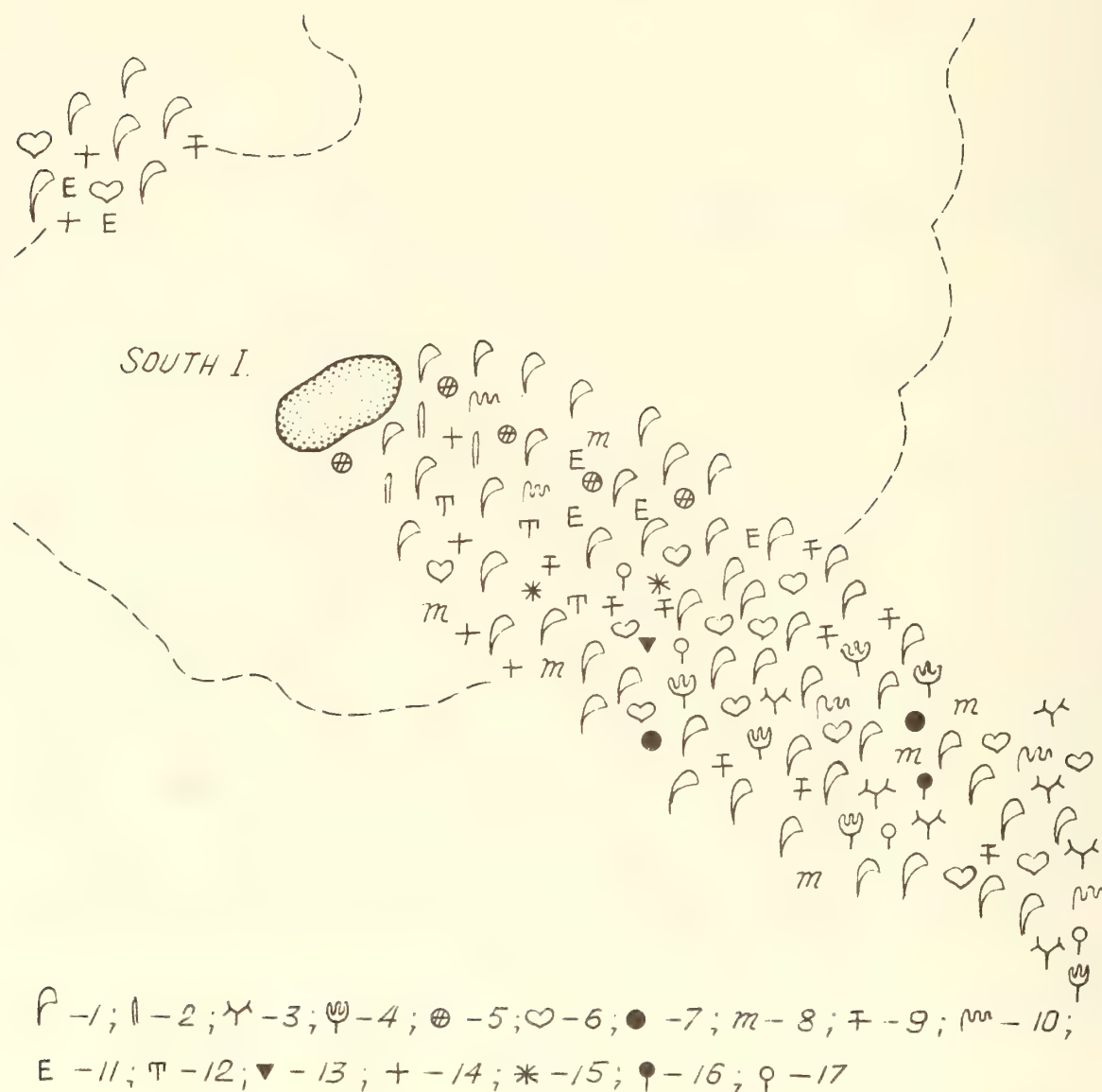


Figure 11. Horizontal distribution of algal and seagrass species of African Banks. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Tricleocarpa oblongata*, 4 - *Avrainvillea amadelpha*, 5 - *Boodlea struveoides*, 6 - *Halimeda* species, 7 - *Lobophora variegata*, 8 - *Valonia fastigiata*, 9 - *Dictyurus purpurascens*, 10 - *Caulerpa* species, 11 - *Dasya mollis*, 12 - *Laurencia* species, 13 - *Turbinaria ornata*, 14 - *Dictyosphaeria* species, 15 - *Porolithon gardineri*, 16 - *Udotea argentea*, 17 - *Rhipilia tomentosa*.

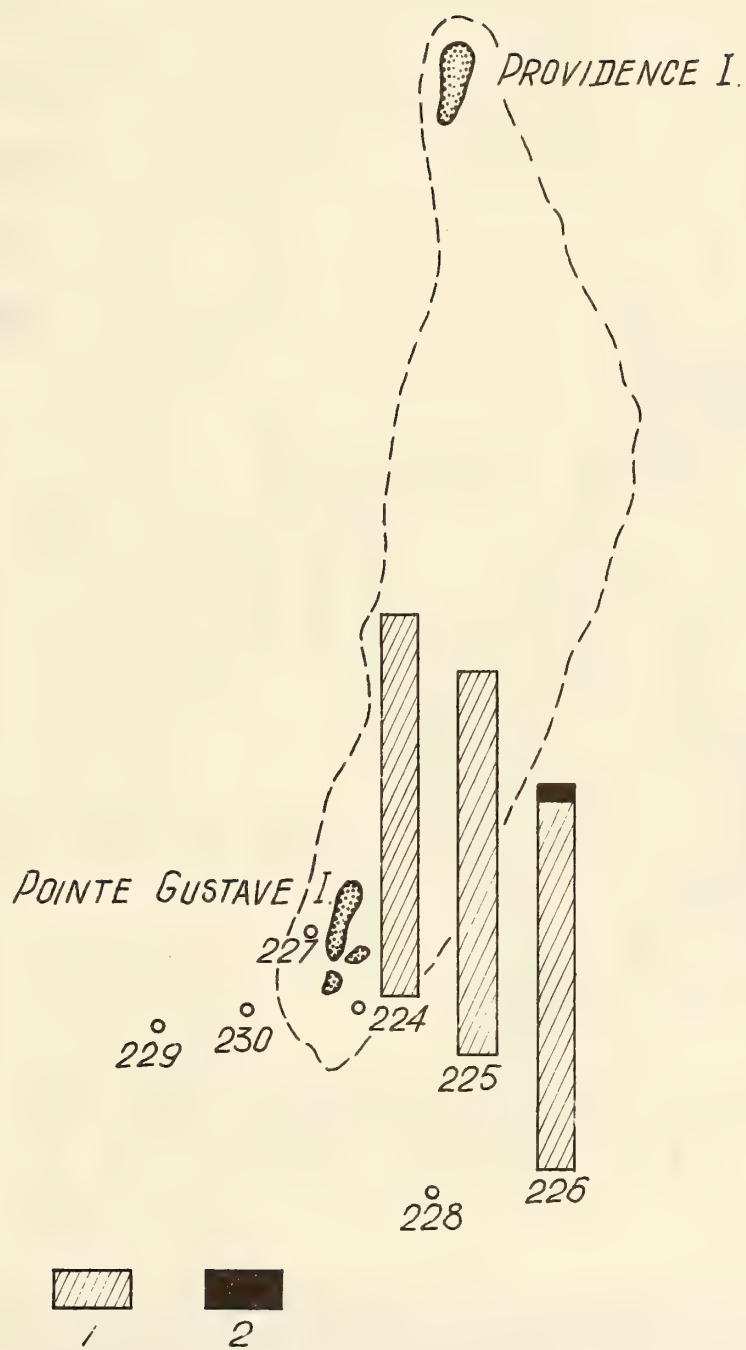
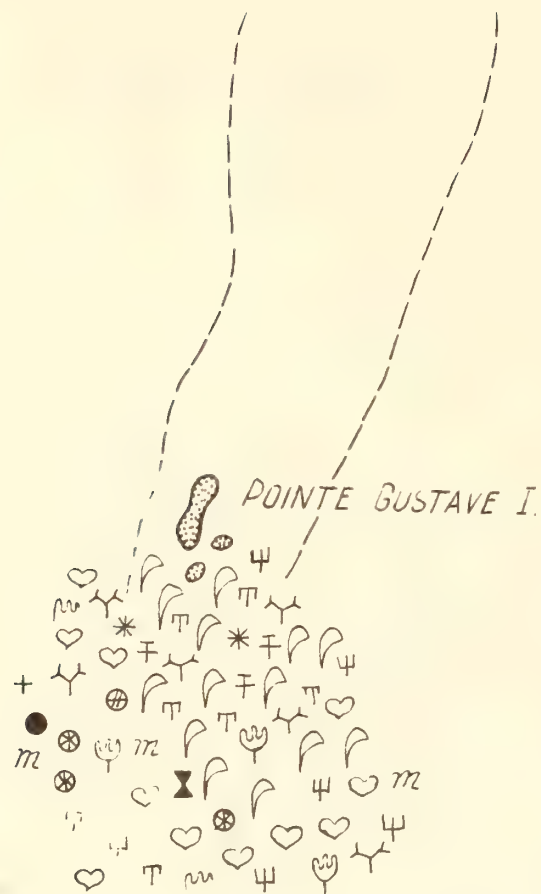


Figure 12. Location of stations and species ratios of phytozoenoses at Providence Island. 1 - *Thalassodendron ciliatum*, 2 - other species.



P-1; ♥-2; ~-3; T-4; +-5; Y-6; u-7; u-8; ⊗-9; m-10;
 ●-11; +-12; ⊠-13; ⊗-14; *-15

Figure 13. Horizontal distribution of algal and seagrass species at Providence Island. 1 - *Thalassodendron ciliatum*, 2 - *Halimeda* species, 3 - *Caulerpa* species, 4 - *Laurencia* species, 5 - *Dictyurus purpurascens*, 6 - *Tricleocarpa oblongata*, 7 - *Microdictyon montagnei*, 8 - *Avrainvillea amadelpha*, 9 - *Jania* species, 10 - *Valonia fastigiata*, 11 - *Lobophora variegata*, 12 - *Dictyosphaeria cavernosa*, 13 - *Haloplegma duperreyi*, 14 - *Boodlea struveoides*, 15 - *Porolithon gardineri*.

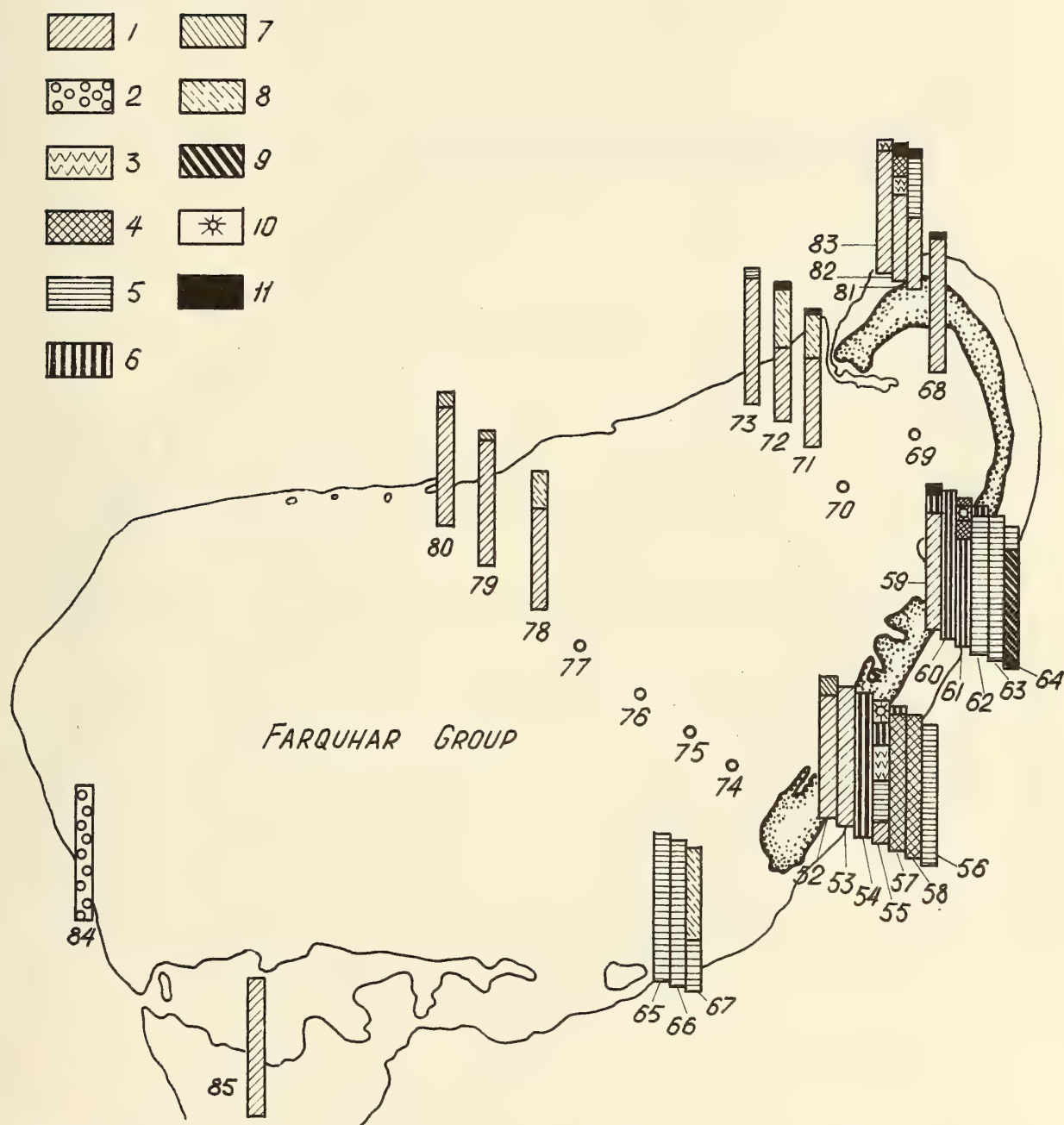


Figure 14. Location of stations and species ratios in phytocoenoses at Farquhar Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Sargassum ilicifolium*, 3 - *Valonia aegagropila*, 4 - *Microdictyon okamurai*, 5 - *Caulerpa cupressoides*, 6 - *Boodlea struveoides*, 7 - *Thalassia hemprichii*, 8 - *Halimeda opuntia*, 9 - *Udotea*, 10 - *Dictyosphaeria cavernosa*, 11 - other minor species.

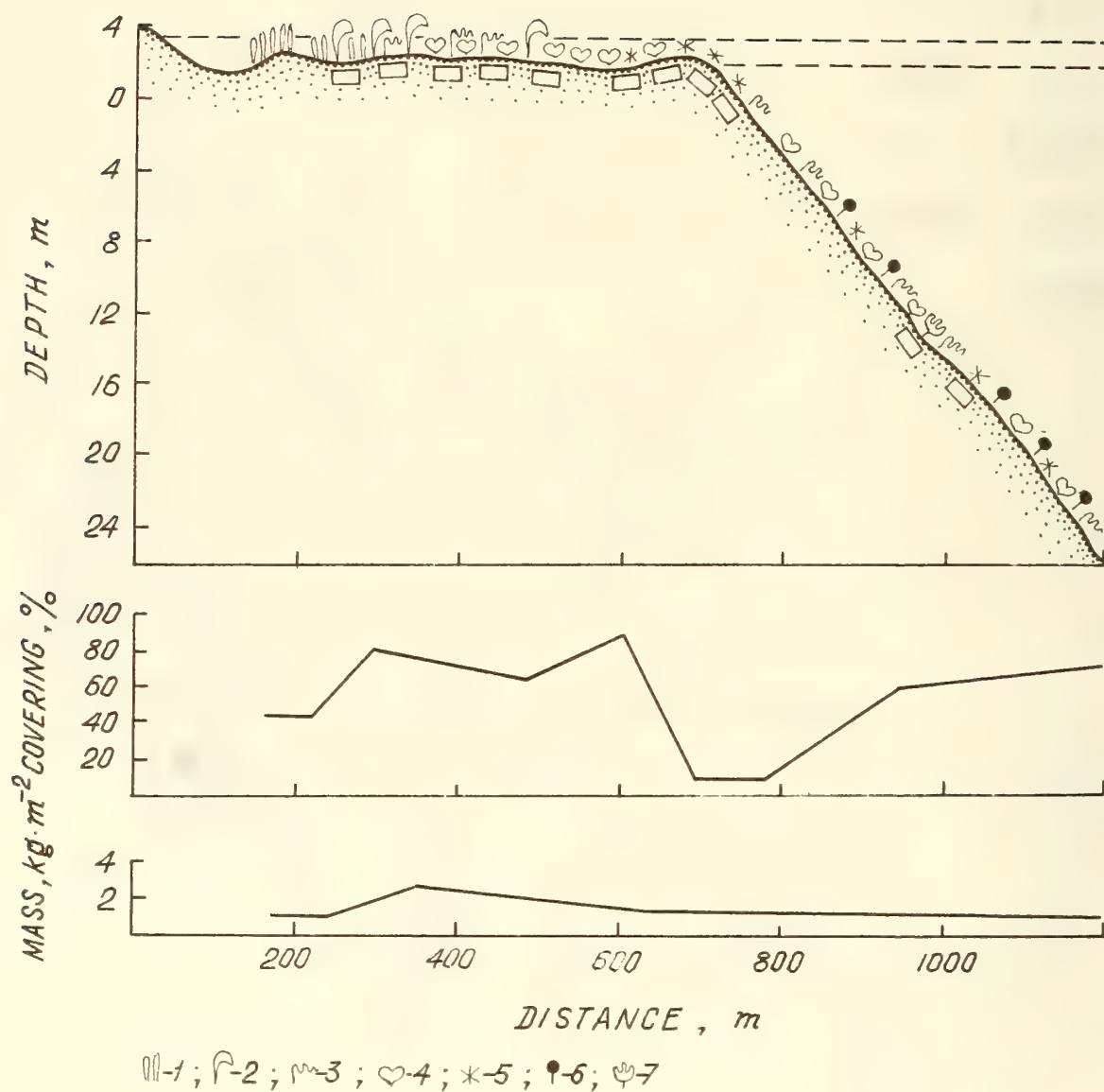


Figure 15. Vertical distribution of dominant species, biomass and percent cover of algae and seagrasses at Farquhar Atoll. 1 - *Thalassia hemprichii*, 2 - *Thalassodendron ciliatum*, 3 - *Caulerpa cupressoides*, 4 - *Halimeda opuntia*, 5 - *Porolithon gardineri*, 6 - *Udotea*, 7 - *Avrainvillea amadelpha*.

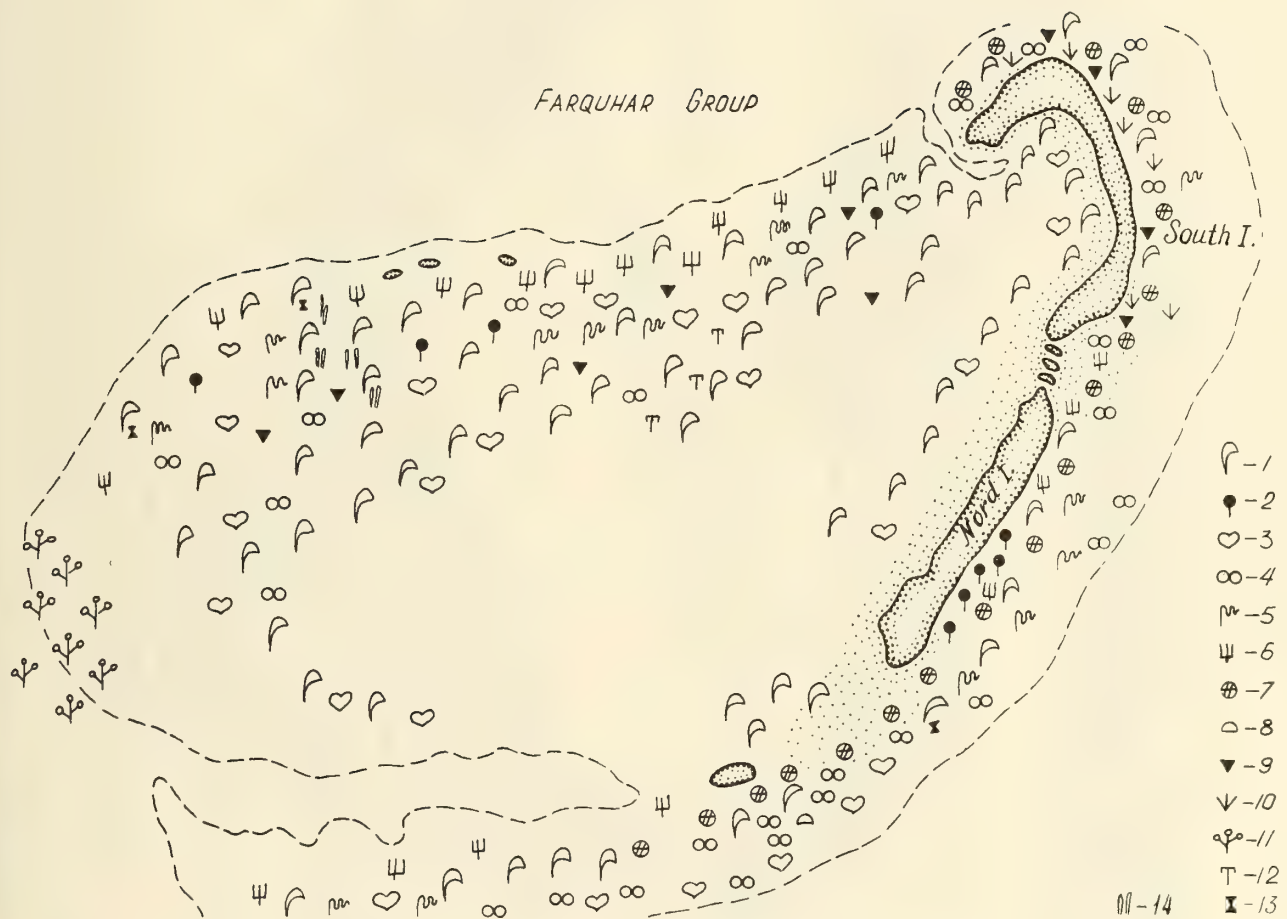


Figure 16. Horizontal distribution of algal and seagrass species at Farquhar Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Udotea*, 3 - *Halimeda* species, 4 - *Valonia aegagropila*, 5 - *Caulerpa cupressoides*, 6 - *Microdictyon okamurai*, 7 - *Boodlea struveoides*, 8 - crustose species, 9 - *Turbinaria ornata*, 10 - *Liagora ceranoides*, 11 - *Sargassum ilicifolium*, 12 - *Laurencia* species, 13 - *Haloplegma dupperreyi*, 14 - *Thalassia hemprichii*.

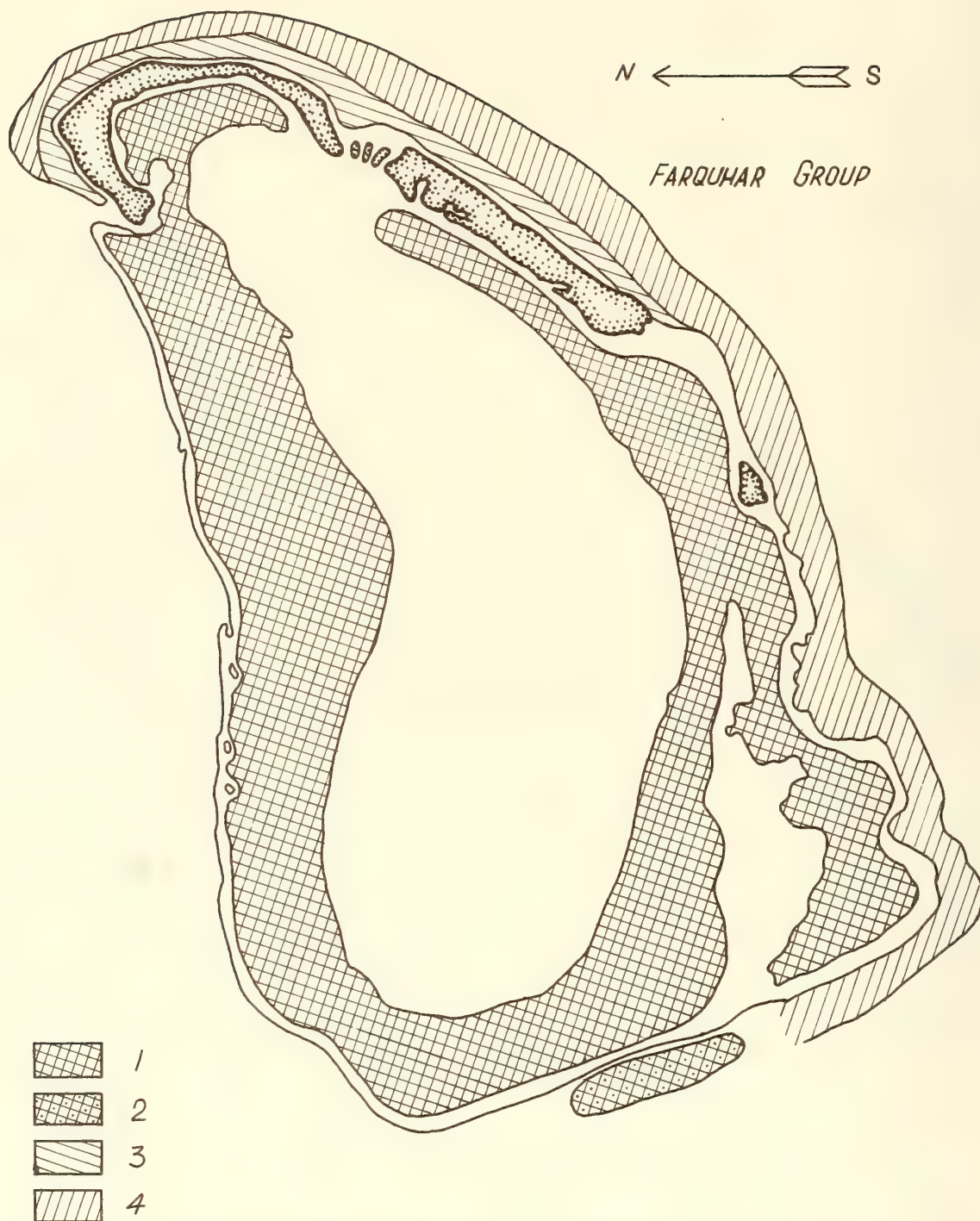


Figure 17. Distribution of macrophyte biomass at Farquhar Atoll (in $\text{g}\cdot\text{m}^{-2}$): 1 - 2508 ± 994 ; 2 - 2880 ; 3 - 1209 ± 300 ; 4 - 303 ± 94 .

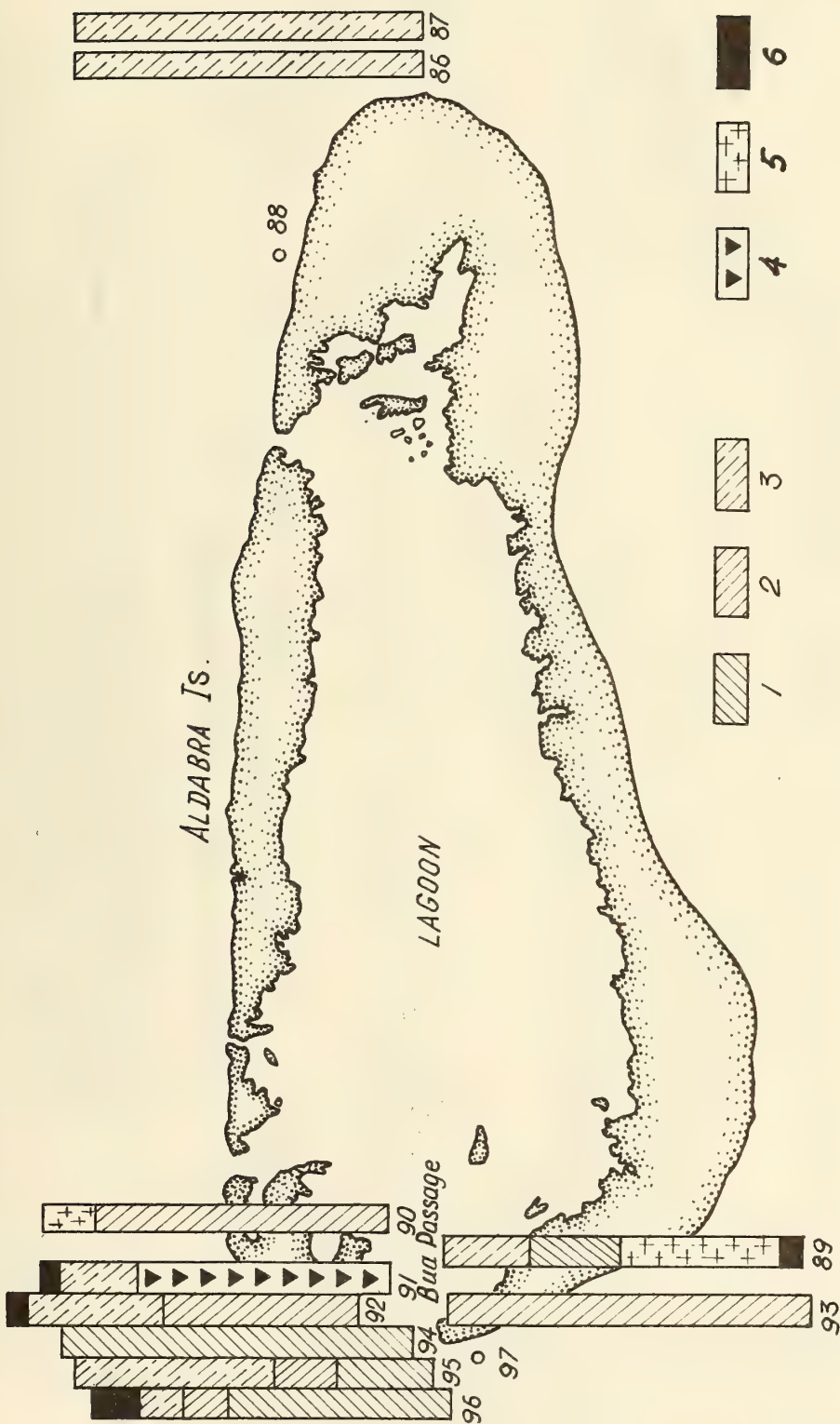


Figure 18. Location of stations and species ratios in phytocenoses at Aldabra Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Halimeda opuntia*, 4 - *Turbinaria ornata*, 5 - *Laurencia* species, 6 - other minor species.

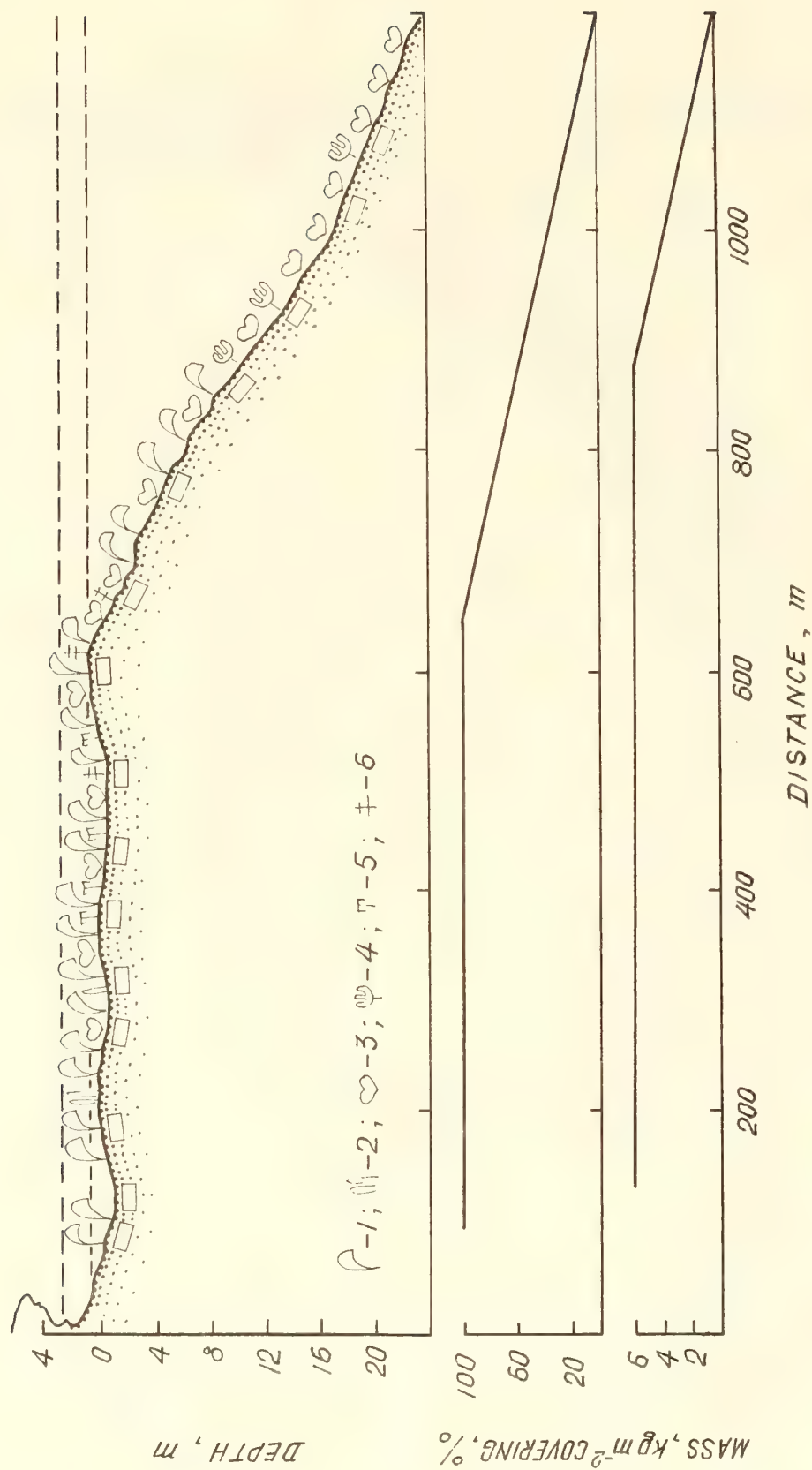


Figure 19. Vertical distribution of dominant species, biomass and percent cover of algae and seagrasses at Aldabra Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Halimeda* species, 4 - *Avrainvillea amadelpha*, 5 - *Laurencia* species, *Dictyurus purpurascens*.

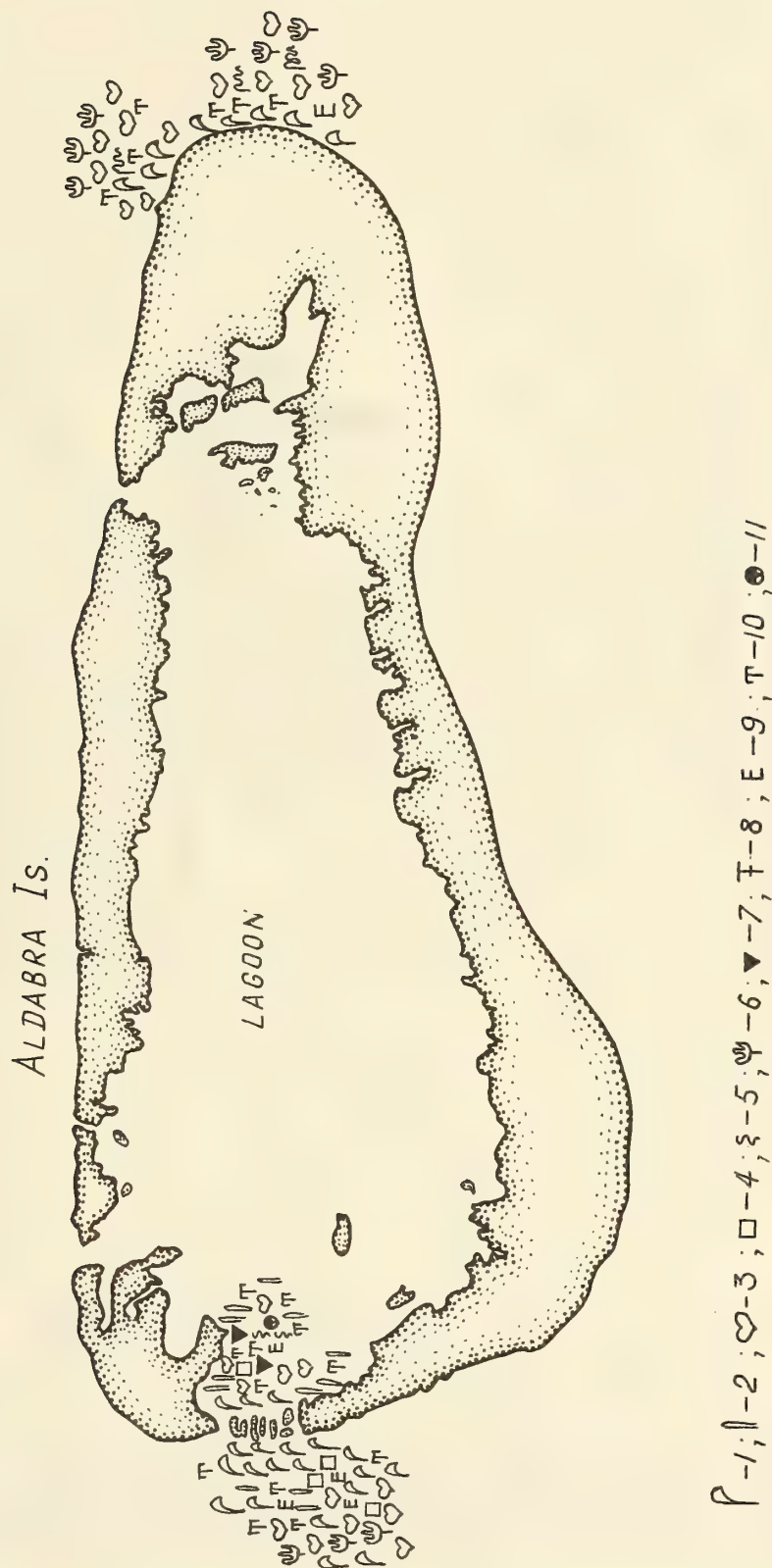


Figure 20. Horizontal distribution of algal and seagrass species at Aldabra Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Halimeda opuntia*, 4 - *Ulva rigida*, 5 - *Enteromorpha kyllini*, 6 - *Avrainvillea amadelpha*, 7 - *Turbinaria ornata*, 8 - *Dictyurus purpurascens*, 9 - *Dasya* species, 10 - *Laurencia* species, 11 - *Spyridia filamentosa*.

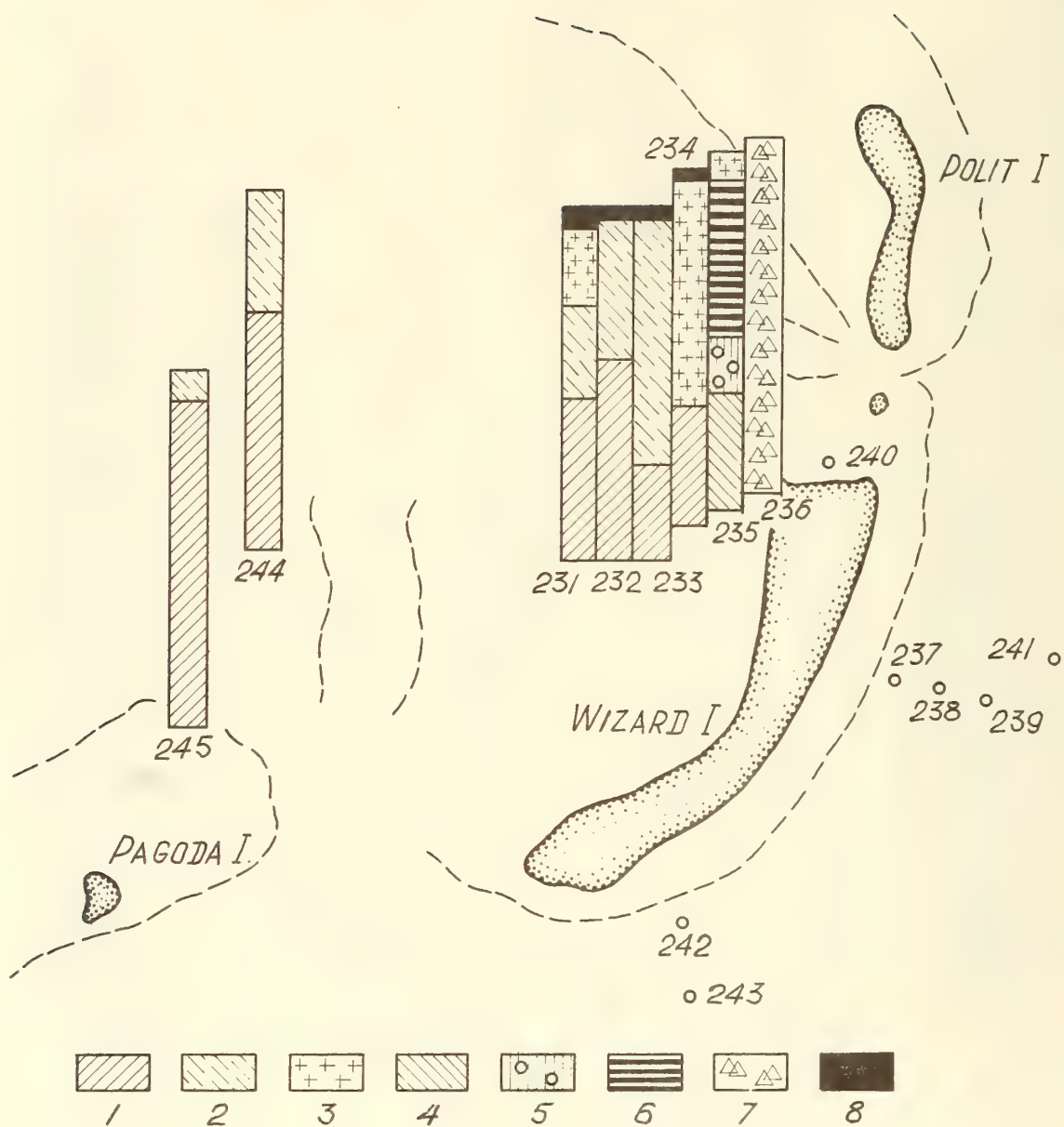


Figure 21. Location of stations and species ratios in phytocoenoses at Cosmoledo Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Halimeda opuntia*, 3 - *Laurencia papillosa*, 4 - *Thalassia hemprichii*, 5 - *Cymodocea serrulata*, 6 - *Jania* species, 7 - *Halodule uninervis*, 8 - other minor species.

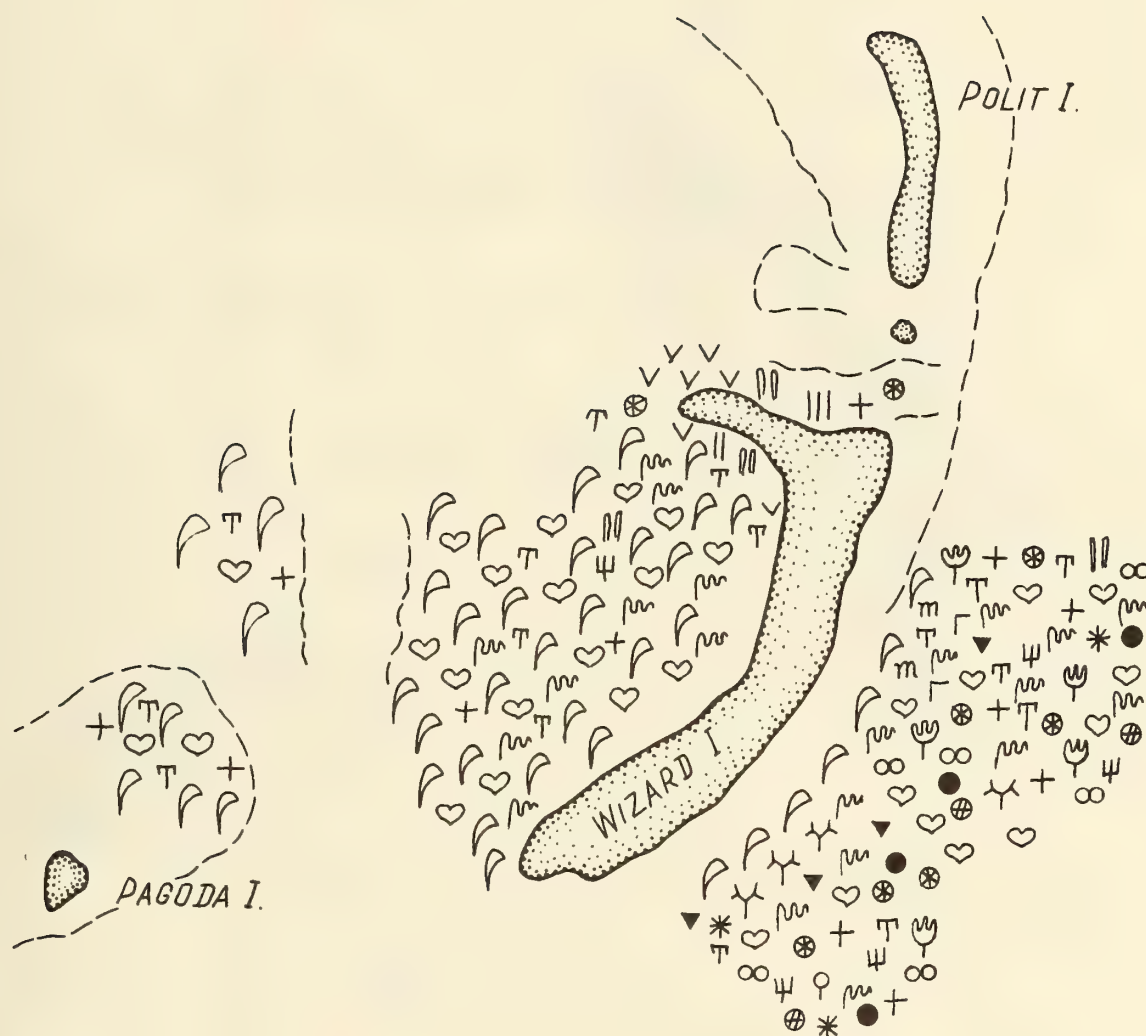


Figure 22. Horizontal distribution of algal and seagrasses at Cosmoledo Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Halimeda opuntia*, 3 - *Laurencia* species, 4 - *Thalassia hemprichii*, 5 - *Cymodocea serrulata*, 6 - *Jania* species, 7 - *Halodule uninervis*, 8 - *Lobophora variegata*, 9 - *Microdictyon okamurai*, 10 - *Caulerpa* species, 11 - *Dictyosphaeria cavernosa*, 12 - *Avrainvillea amadelpha*, 13 - *Hypnea* species, 14 - *Tricleocarpa oblongata*, 15 - *Turbinaria ornata*, 16 - *Valonia fastigiata*, 17 - *Boodlea struveoides*, 18 - *Porolithon gardineri*, 19 - *Rhipilia tomentosa*, 20 - *Valonia aegagropila*.

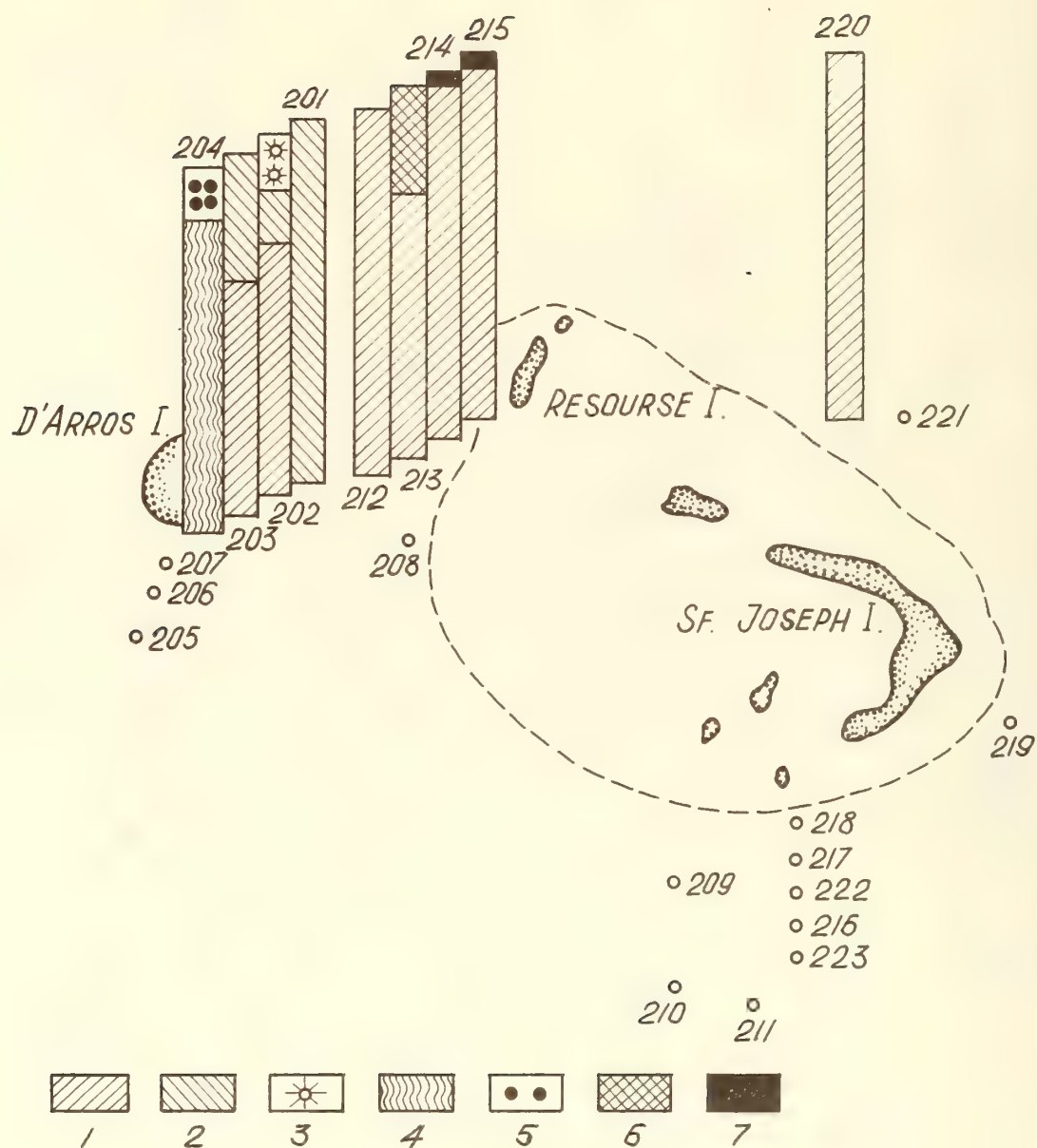


Figure 23. Location of stations and species ratios in phytocoenoses at St. Joseph Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Dictyosphaeria* species, 4 - *Cladophoropsis sundanensis*, 5 - *Valonia* species, 6 - *Microdictyon* species, 7 - other minor species.

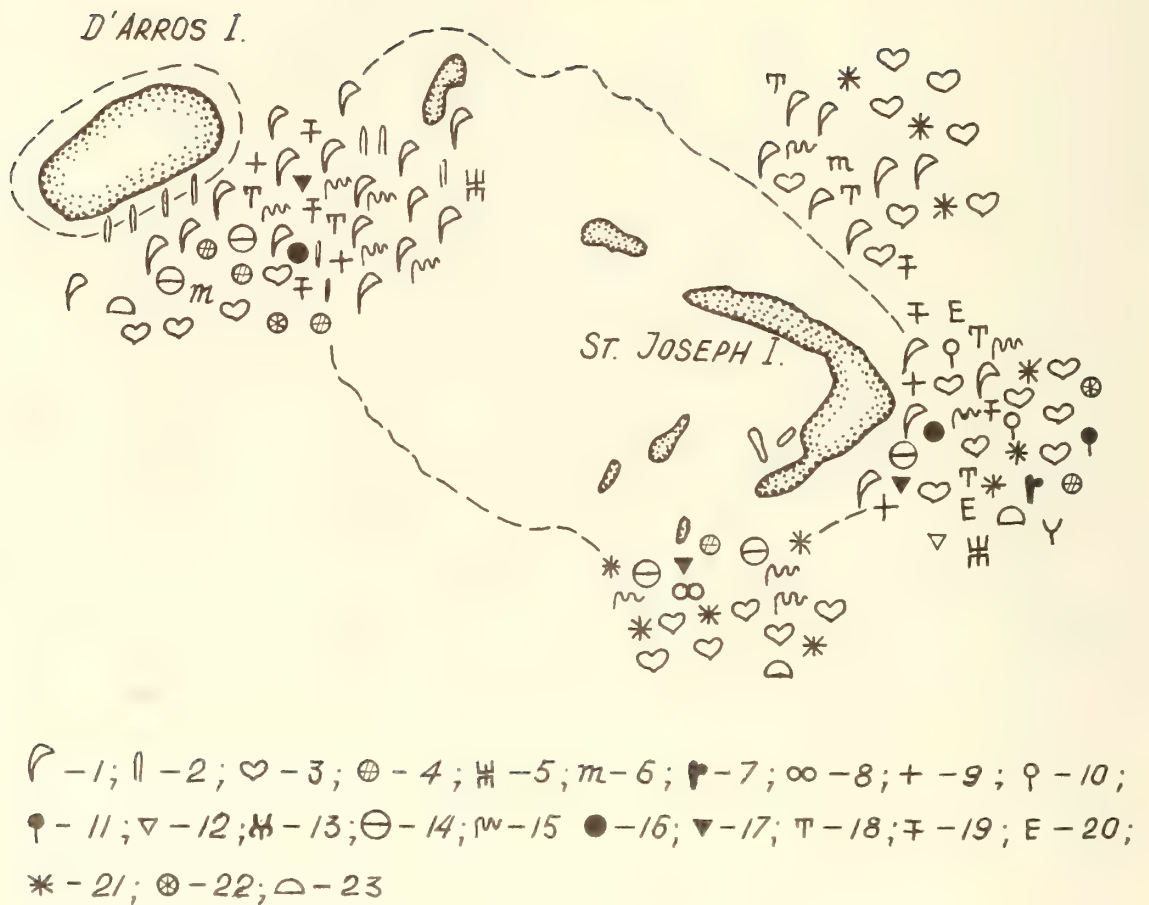


Figure 25. Horizontal distribution of algal and seagrass species at St. Joseph Atoll. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Halimeda* species, 4 - *Boodlea struveoides*, 5 - *Microdictyon montagnei*, 6 - *Valonia fastigiata*, 7 - *Valonia utricularis*, 8 - *Valonia aegagropila*, 9 - *Dictyosphaeria* species, 10 - *Rhipilia tomentosa*, 11 - *Udotea argentea*, 12 - *Udotea orientalis*, 13 - *Codium* species, 14 - *Cladophoropsis sundanensis*, 15 - *Caulerpa* species, 16 - *Lobophora variegata*, 17 - *Turbinaria ornata*, 18 - *Laurencia* species, 19 - *Dictyurus purpurascens*, 20 - *Dasys mollis*, 21 - *Sporolithon sporolithon*, 22 - *Jania* species, 23 - crustose species.

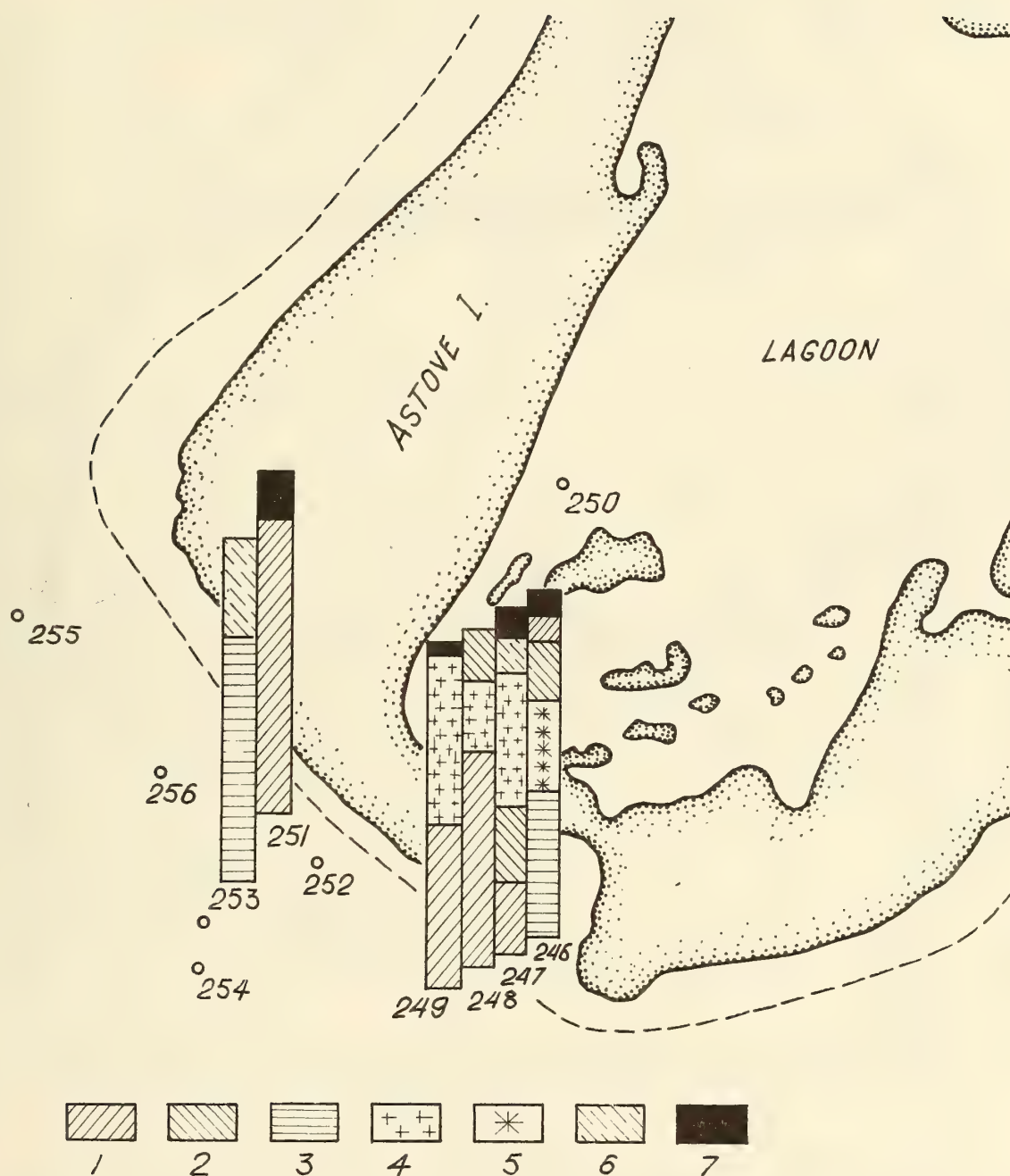


Figure 26. Location of stations and species ratios in phytocoenoses at Astove Island. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Caulerpa* species, 4 - *Laurencia* species, 5 - *Amphiroa*, 6 - *Halimeda* species, 7 - other minor species.

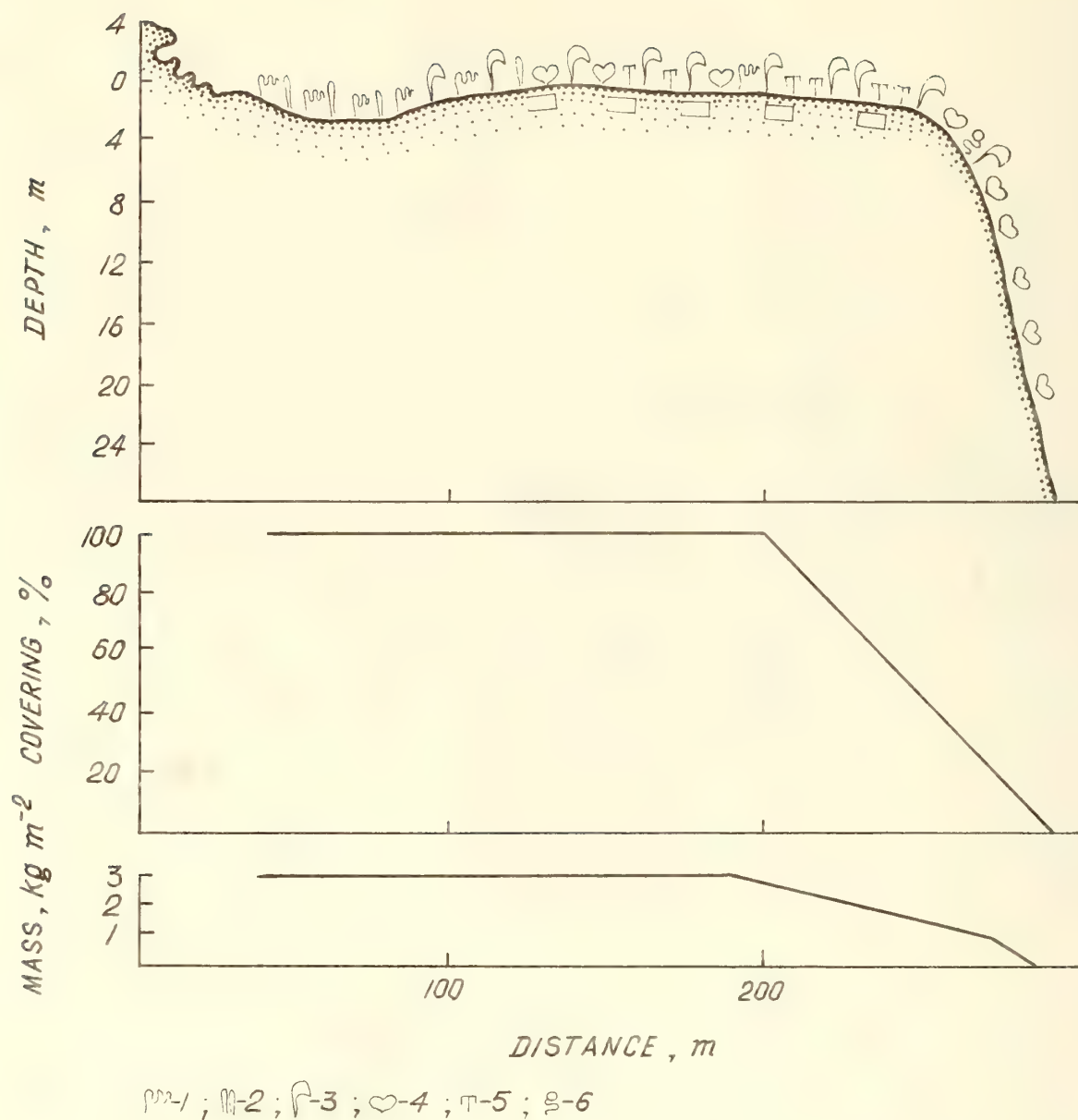
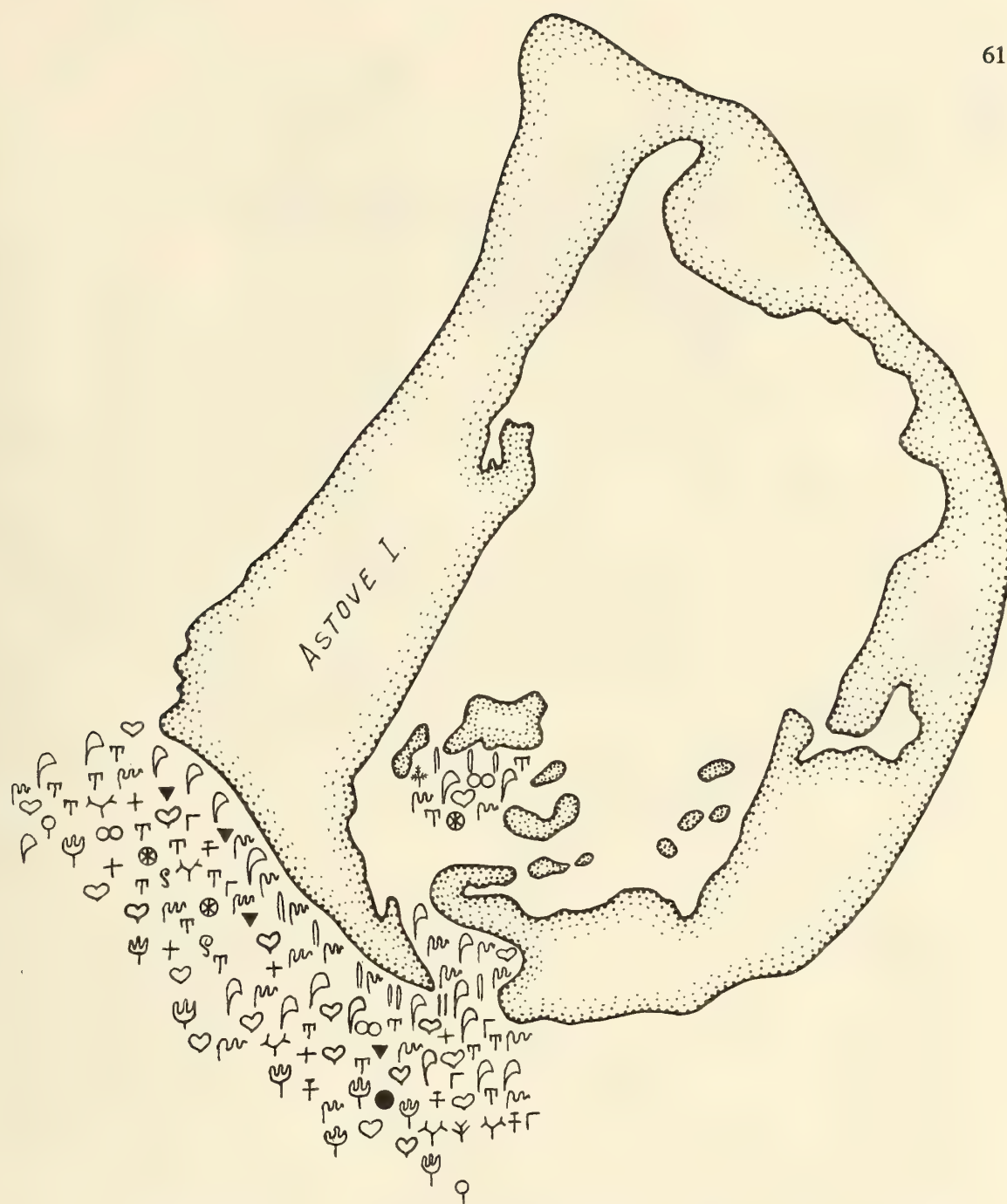


Figure 27. Vertical distribution of dominant species, biomass and percent cover of algae and seagrasses at Astove Island. 1 - *Caulerpa* species, 2 - *Thalassia hemprichii*, 3 - *Thalassodendron ciliatum*, 4 - *Halimeda* species, 5 - *Laurencia* species, 6 - *Iagora* species.



|| -1; P -2; || -3; ♥ -4; ~ -5; + -6; ♀ -7; ∞ -8; Ψ -9; ▼ -10;

● -11; T -12; † -13; Γ -14; Y -15; Ψ -16; ⊗ -17; S -18; * -19

Figure 28. Horizontal distribution of algal and seagrass species at Astove Island. 1- *Thalassia hemprichii*, 2 - *Thalassodendron ciliatum*, 3 - *Halodule uninervis*, 4 - *Halimeda* species, 5 - *Caulerpa* species, 6 - *Dictyosphaeria* species, 7 - *Rhipilia tomentosa*, 8 - *Valonia aegagropila*, 9 - *Avrainvillea amadelpha*, 10 - *Turbinaria ornata*, 11 - *Lobophora variegata*, 12 - *Laurencia* species, 13 - *Dictyurus purpurascens*, 14 - *Hypnea spinella*, 15 - *Galaxaura* species, 16 - *Heterosiphonia* species, 17 - *Jania* species, 18 - *Liagora* species, 19 - *Spyridia filamentosa*.

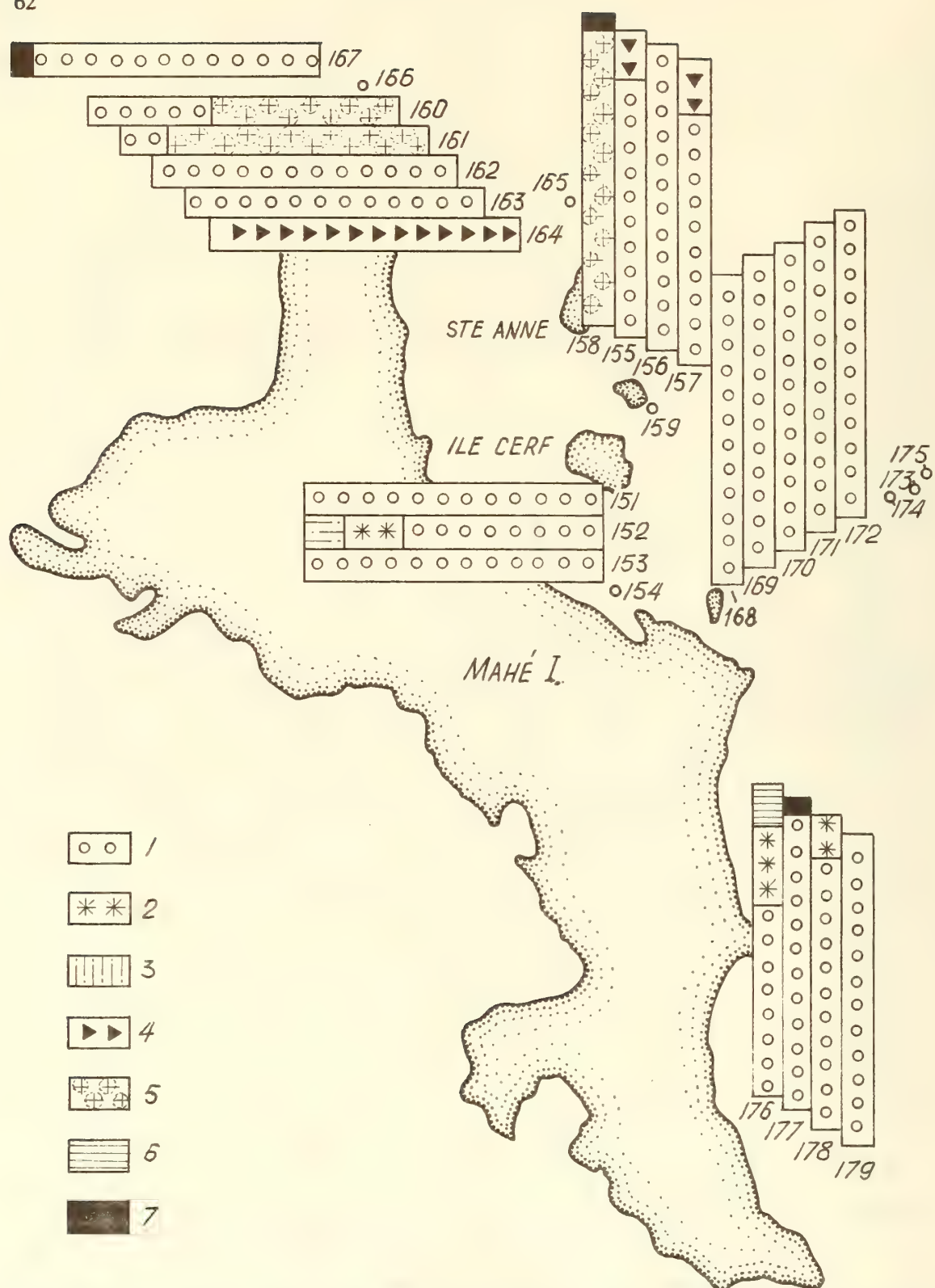


Figure 29. Location of stations and species ratios in phytocoenoses at Mahé Island. 1 - *Sargassum* species, 2 - *Amphiroa foliacea*, 3 - *Gelidiella acerosa*, 4 - *Turbinaria decurrens*, 5 - *Gracilaria* species, 6 - *Caulerpa racemosa*, 7 - other minor species.

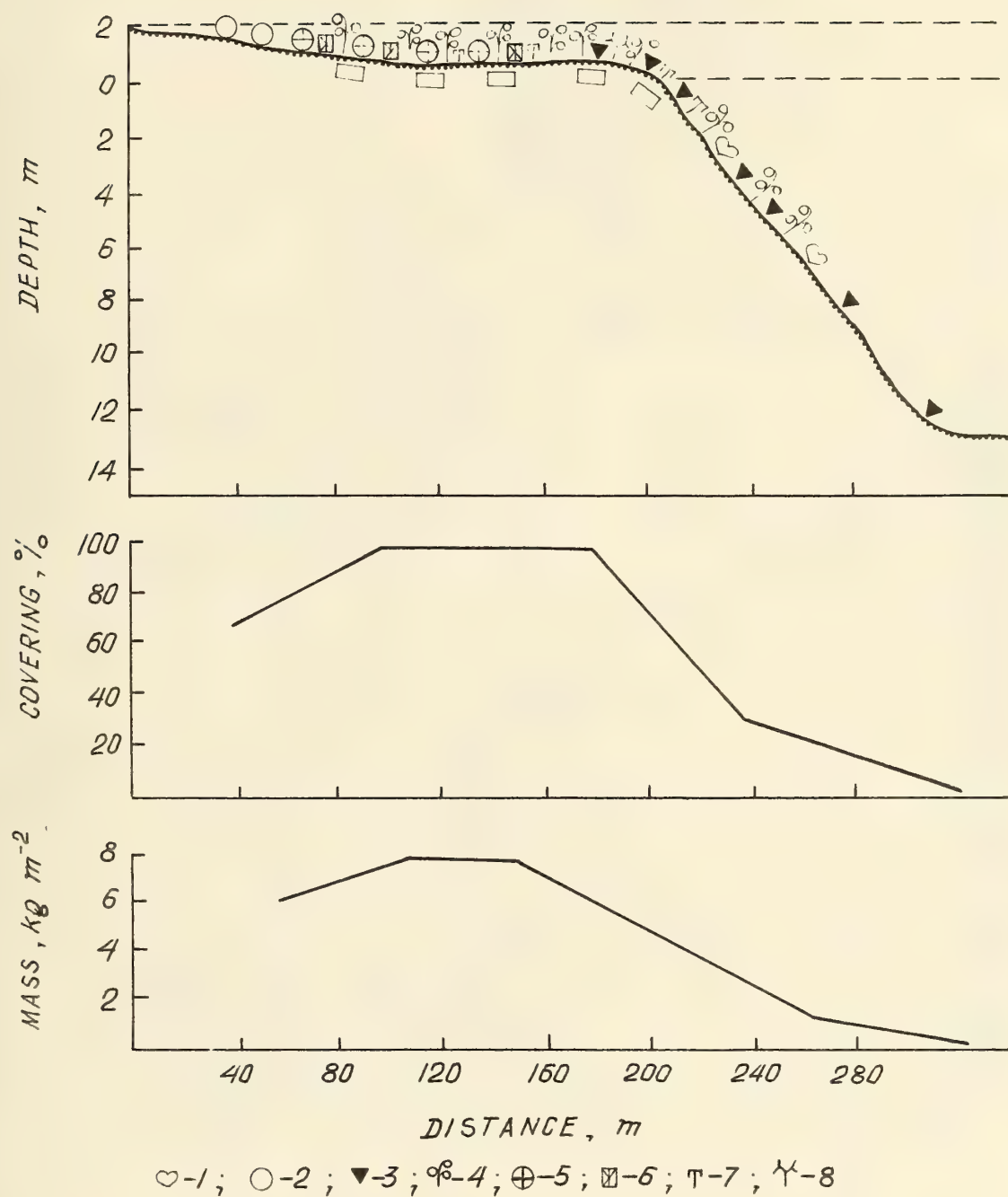


Figure 30. Vertical distribution of dominant species, biomass and percent cover of algae and seagrasses at Mahé Island. 1 - *Halimeda*, 2 - *Padina* species, 3 - *Turbinaria* species, 4 - *Sargassum* species, 5 - *Gracilaria* species, 6 - *Amphiroa foliacea*, 7 - *Laurencia* species, 8 - *Tricleocarpa oblongata*.



Figure 31. Horizontal distribution of algal and seagrass species at Mahé Island. 1 - *Thalassodendron ciliatum*, 2 - *Cymodocea serrulata*, 3 - *Halimeda* species, 4 - *Caulerpa racemosa*, 5 - *Ulva rigida*, 6 - *Dictyota* species, 7 - *Turbinaria* species, 8 - *Padina* species, 9 - *Lobophora variegata*, 10 - *Sargassum* species, 11 - *Gracilaria* species, 12 - *Amphiroa foliacea*, 13 - *Hypnea* species, 14 - *Gelidiella acerosa*, 15 - *Tricleocarpa oblongata*, 16 - *Laurencia* species, 17 - *Halodule uninervis*.

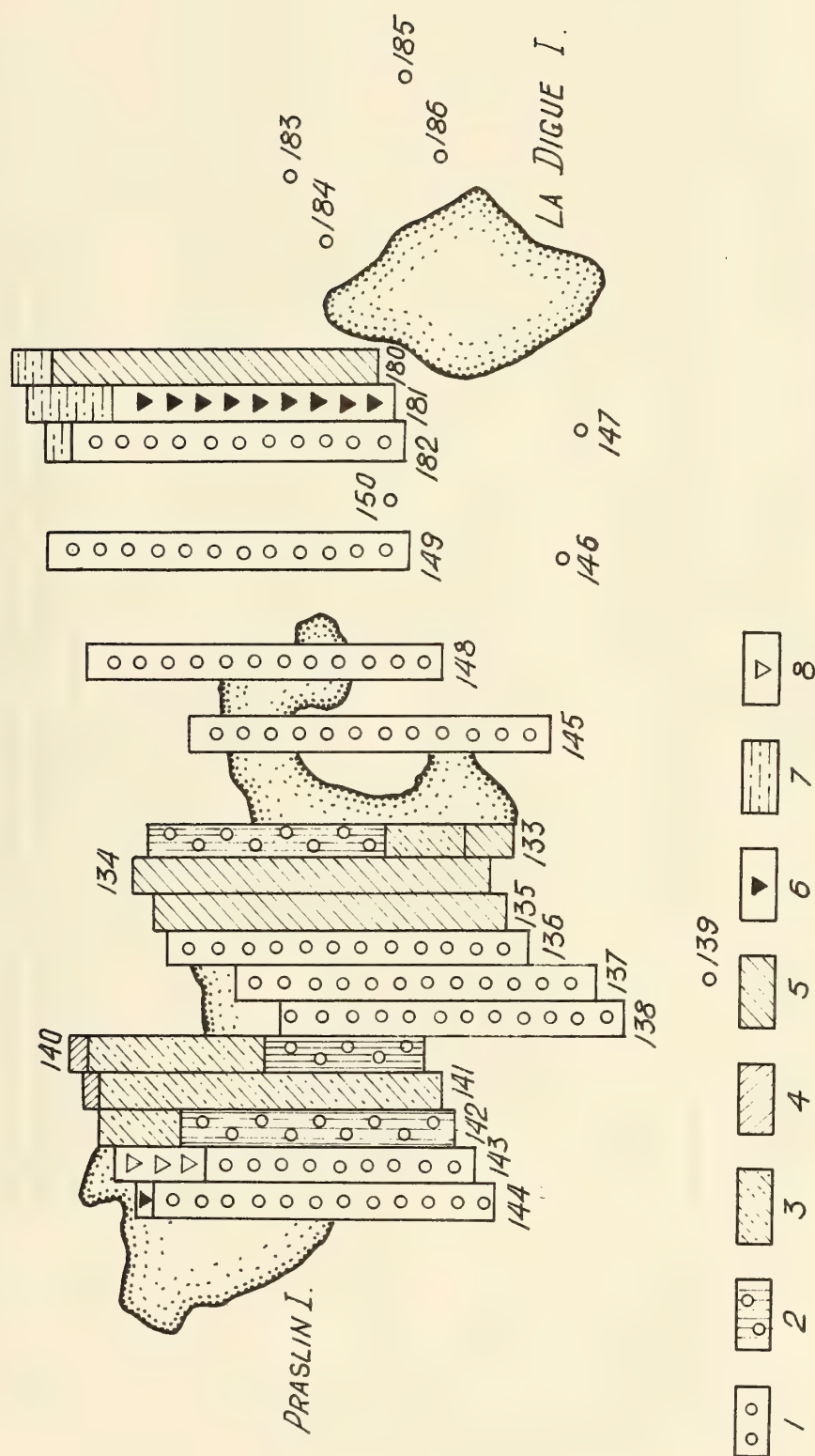


Figure 32. Location of stations and species ratios in phytocoenoses at Praslin and La Digue Islands.
 1 - *Sargassum* species, 2 - *Cymodocea serrulata*, 3 - *Syringodium isoetifolium*, 4 - *Thalassia hemprichii*, 5 - *Turbinaria* species, 7 - *Hypnea pannosa*, 8 - *Padina* species.

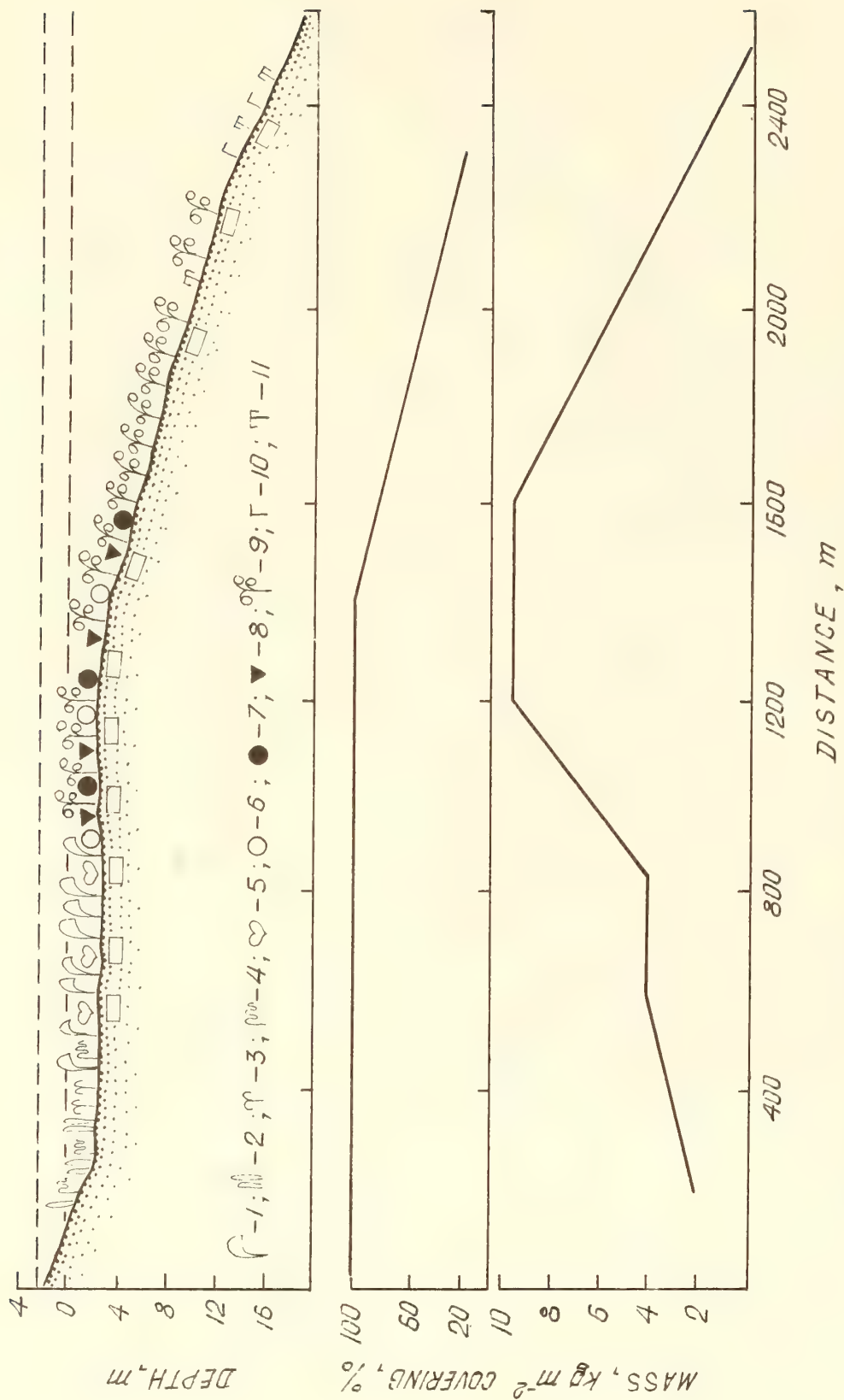


Figure 33. Vertical distribution of dominant species, biomass and percent cover of algae and seagrasses at Praslin Island. 1 - *Thalassodendron ciliatum*, 2 - *Thalassia hemprichii*, 3 - *Syringodium isoetifolium*, 4 - *Caulerpa serrulata*, 5 - *Halimeda* species, 6 - *Padina* species, 7 - *Lobophora variegata*, 8 - *Turbinaria* species, 9 - *Sargassum* species, 10 - *Hypnea* species, 11 - *Laurencia* species.



Figure 34. Horizontal distribution of species of algae and seagrasses at Praslin and La Digue Islands.

1 - *Halodule uninervis*, 2 - *Thalassia hemprichii*, 3 - *Syringodium isoetifolium*, 4 - *Thalassodendron ciliatum*, 5 - *Cymodocea serrulata*, 6 - *Halophila ovalis*, 7 - *Halimeda macroloba*, 8 - *Dictyosphaeria cavernosa*, 9 - *Caulerpa* species, 10 - *Lobophora variegata*, 11 - *Turbinaria* species, 12 - *Dictyota* species, 13 - *Dictyopteris polypodioides*, 14 - *Turbinaria* species, 15 - *Sargassum* species, 16 - *Laurencia* species, 17 - *Hypnea* species, 18 - *Heterosiphonia* species, 19 - *Gracilaria crassa*, 20 - crustose species.

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**CHAPTER 6
FOULING COMMUNITIES OF THE
SEYCHELLES ISLANDS
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CHAPTER 6
FOULING COMMUNITIES OF THE
SEYCHELLES ISLANDS

BY
A.Y. Zvyagintsev* and V.V. Ivin*

INTRODUCTION

The phenomenon of fouling is foremost among the problems presented by the deterioration of man-made objects in the sea (Reznichenko et al. 1976). The Seychelles are subjected to fouling as in other tropical coastal areas; however, to date no investigation of fouling on hydrotechnical constructions (HTC) and inter-island trade vessels (ITV) has been undertaken for the region. The fouling of an ocean-going vessel during its passage from this region to the coast of Vietnam was studied by Zvyagintsev and Mikhailov (1985).

Manmade objects near Farquhar, Aldabra, Desroches, Praslin and Mahé Islands were surveyed. A major part of the material was collected in Victoria Harbor (Mahé Island). The study focused on algal fouling communities and included the following:

- 1) Identification of fouling algal flora which considerably expands the list of algae for this region.
- 2) Comparison of the lists of fouling and epiphyton species to determine the role of epiphyton as a potential source of foulers for artificial substrata.
- 3) Identification of fouling species to forecast fouling in different habitats.
- 4) Knowledge of common algal and animal fouling species also may be useful in cultivating these species on anthropogenic substrata.

The rate of fouling on cleaned versus fouled surfaces of vessel hulls was compared to determine the efficiency of underwater cleaning in tropical waters. Observations were made on survival of the algae introduced from boreal waters.

METHODS AND MATERIALS

During the expedition 6 ITVs, 7 HTCs and the underwater surface foulings on the hull of the R/V Akademik A. Nesmeyanov were surveyed. Eighty quantitative and 14 qualitative samples were taken and analyzed in the laboratory by the methods of Zadin (1969). Five 1 m² experimental quadrats were cleaned at various depths below the waterline, according to the techniques given in Litvin et al. (1979). Quantitative samples (wet wt) were taken every 15 days from 0.04 m² of fouled (control) and cleaned surfaces simultaneously. Samples were collected using SCUBA diving in a manner similar to that of Zvyagintsev and Mikhailov (1980) and Kashin (1982).

Algae were identified to species when possible, invertebrates were generally identified to higher

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taxonomic units. A comparison of the qualitative composition of the flora of fouling and epiphyton was made using cluster analysis (Andreev 1980). Samples of the common species of fouling algae were given to specialists of the expedition's Biochemistry and Physiology groups for further research.

RESULTS

Farquhar Island

A submerged vessel at the southeastern bank was examined under conditions of strong wave activity. The sea bottom was flat with the brown alga *Sargassum* growing on the surrounding dead coral substratum. The vessel had rested on the 0-4 m deep bottom since 1975. The entire hull was covered with a layer of powdery corrosion about 3 mm thick.

A community of 8 algal and 13 animal species was found on the vessel's hull below the waterline (Table 1). The community biomass consisted of 95.5% algae ($1721 \text{ g}\cdot\text{m}^{-2}$ at the waterline). Two algal species, *Jania unguolata* and *Struvea anastomosans*, dominated the biomass (57 and 38% of the total biomass, respectively) and *Ulva rigida* was a common species (3%). In spite of high species richness, the total faunistic biomass was very low (0.5%). Motile forms such as crustaceans and molluscs predominated. Maximal population density was $2000 \text{ individuals}\cdot\text{m}^{-2}$. Representatives of other groups were found as single individuals or in the qualitative samples. The same community with approximately half the total biomass was found at the 2 m depth. At a depth of 4 m, *Sargassum ilicifolium* became the predominant species (91% of the total wet biomass, $5228 \text{ g}\cdot\text{m}^{-2}$) fouling the horizontal steel surfaces of the hull. Subdominants included the same algal species as above with fewer motile animals.

Aldabra Island

A navigational buoy with a chain installed above 20 m was studied. The underwater surface of the buoy was free of fouling, probably because of an antifouling coating. The steel chain was fouled from 0 to 15 m in depth and no foulings occurred deeper. The species included 21 algae but only *Ulva rigida* provided appreciable biomass (Table 2). Red algae were responsible for most of the diversity with the maximum numbers of species at 1 m in depth. Among the six animal species. The cirripedia *Lepas anatifera* strongly dominated the biomass, while other species occurred rarely. Communities of *L. anatifera* and *U. rigida* occurred with alternating predominances from 0 to 15 m in depth while the total biomass gradually decreased with increasing depth.

Desroches Island

A navigational buoy at a yacht mooring was examined over a 3 m depth range. The underwater parts of the steel surface had no protective coating and were corroded. The buoy surface was completely covered by algal foulings, which included 31 species with red algae predominating (Table 3). *Enteromorpha* and *Polysiphonia* accounted for most of the total biomass (420 and $380 \text{ g}\cdot\text{m}^{-2}$, respectively), other algae were sparse. Among the 10 animal species, *Lepas anatifera* was responsible for 99% of the total biomass ($670 \text{ g}\cdot\text{m}^{-2}$, at a population density of $1100 \text{ individuals}\cdot\text{m}^{-2}$). Algal growths were inhabited by many crustaceans, molluscs and polychaetes. No macrofouling was found on the line connecting the buoy to its anchor.

Praslin Island

A concrete pier at a depth to 2 m was surveyed. Its fouling community contained 20 algal and 18 animal species (Table 4). Red algae were the most diverse in the community, with *Peyssonnelia* sp. contributing the most biomass ($22.5 \text{ g}\cdot\text{m}^{-2}$). Faunistically, the barnacle *Tetraclita squamosa* dominated (up to $5250 \text{ g}\cdot\text{m}^{-2}$), with sponges and actinians occurring as subdominants. Biomass of motile crustaceans and gastropods did not exceed $2 \text{ g}\cdot\text{m}^{-2}$. Qualitative samples contained scleractinian corals of the genera *Acropora*, *Favia* and *Pocillopora*. There was a difference in the quantitative samples taken from the pier's protected side compared with the side exposed to wave action, whereas the biomass sharply increased. Fouling decreased with increasing depth.

Victoria Harbor

Two navigational buoys with chains, a pier with steel constructions and 6 different ITVs were studied. An inlet buoy installed near Cerf Island, anchored at a depth of 15 m contained a fouling community that included 13 algal species (9 red algae) and 21 animal species (Table 5). Brown algae ($2500 \text{ g}\cdot\text{m}^{-2}$) were responsible for the bulk of total biomass from 0-1 m in depth, while the total biomass of red algae did not exceed $1 \text{ g}\cdot\text{m}^{-2}$. From 1 m depth and deeper along the entire chain length, a community of the barnacle *Megabalanus tintinnabulum* developed, with a biomass ranging from 9100 to $19200 \text{ g}\cdot\text{m}^{-2}$ and a maximal population density of $3360 \text{ individuals}\cdot\text{m}^{-2}$. The pearl oyster *Pinctada margaritifera* occurred most frequently among the 4 other bivalve molluscs with a biomass of $16400 \text{ g}\cdot\text{m}^{-2}$ at 2 m in depth. Subdominants included *Ascidia* colonies, whose biomass increased with depth. Maximal population densities of motile animals ($4300 \text{ individuals}\cdot\text{m}^{-2}$ for amphipods) was recorded on the buoy within the stands of brown algae.

A mooring buoy (300 m from the pier) had only 2 algal fouling species with *Feldmania breviarticulata* dominating ($460 \text{ g}\cdot\text{m}^{-2}$). Species were similar to those of the inlet buoy but with a different quantitative composition (Table 6). The buoy chain was fouled along its entire length by the oyster *Ostrea* sp. with a biomass of up to $15200 \text{ g}\cdot\text{m}^{-2}$ at 10 m in depth. The cirripedia *Megabalanus tintinnabulum* dominated between 5-10 m in depth. In shallow waters *M. tintinnabulum* was replaced by *Balanus reticulatus*. Ascidians, crustaceans and polychaetes also occurred in great numbers. The pearl oyster was found only in the qualitative samples.

Algae did not occur in the fouling communities on steel constructions characterized by powdery corrosion. Instead, oyster communities predominated with up to $26 \text{ kg wet wt}\cdot\text{m}^{-2}$ and decreased with increasing depth. In comparison with the community of the buoy, the species of both attached and motile forms decreased (Table 7). Sediments of organic origin were abundant in all samples.

The fouling communities of a barge (inactive suction dredger) were similar to those of the pier (Table 8). At the level of the waterline (1 m), there were 4 algal species with *Feldmania breviarticulata* predominating ($620 \text{ g}\cdot\text{m}^{-2}$). The fauna included 19 species, the small barnacle *Balanus reticulatus* predominated at the waterline, and deeper it was replaced by the oyster *Ostrea* sp. (up to $4800 \text{ g}\cdot\text{m}^{-2}$, $2000 \text{ individuals}\cdot\text{m}^{-2}$). These two species comprised the bulk of the total biomass in this community. Motile forms occurred rarely and only in the qualitative samples.

Macrofoulings were not found on the four operational vessels examined. Only a self-propelled hull supported a mixed community of the small cirripedia *Balanus reticulatus*, biomass not exceeding $26 \text{ g}\cdot\text{m}^{-2}$ at the highest population density of $4200 \text{ individuals}\cdot\text{m}^{-2}$. At the waterline, the green alga *Enteromorpha clathrata* dominated (biomass of $145 \text{ g}\cdot\text{m}^{-2}$) and no algae were found deeper (Table 9).

During five consecutive surveys, a succession of fouling communities was observed on the hull of

the R/V Akademik A. Nesmeyanov. On 12 January 1989 at Cœtivy Island, the fouling community was represented by two algal species: *Enteromorpha linza* and *Cladophora laetevirens*. After two weeks, at the same average biomass of algae, the cirripedia *Lepas anatifera* settled with a population density which was about three times higher than on the cleaned experimental surfaces (Table 10). Quantitative sampling revealed many motile crustaceans in the *Enteromorpha* beds. After transit to Mombasa (Kenya), a sharp decrease of *L. anatifera* was observed concurrent with a 2-fold increase in the biomass of *Enteromorpha*. On 23 January 1989 in Victoria Harbor, a decline in abundance of *Enteromorpha* occurred and the remaining plants showed morphological anomalies. The last observation on 14 March 1989 revealed that the normal thallus morphology and biomass of *Enteromorpha* was completely restored.

Fouling communities during the study provided 65 algal species (about 25% of the total algal species in the natural benthos) and 36 animal taxa. Maximum species diversity was represented by the red algae (47 species). The marine flora of the Seychelles was supplemented by some species found only on substrata of anthropogenic origin.

DISCUSSION

It is difficult to compare data of different authors who study sedentary organisms on various substrata. The use of the term "fouling" for communities of organisms inhabiting solid substrata of different origins is being widely discussed in the Soviet literature (e.g., Reznichenko et al. 1976, Protasov 1982, Seravin et al. 1985, Galtsova et al. 1985). As a rule, most authors deal with solid non-living substrata of either artificial or natural origin. However, they avoid analysis of attached communities on living substrata (algal thalli, stems and leaves of seagrasses, valves and shells of molluscs), although the question of epiphytism needs resolution. Zernov (1934) suggested two different Russian terms: "narost" for living and "obrost" for non-living substrata, but these terms have not been generally accepted. A majority of works, devoted to communities of epibionts and borers of molluscan valves use the term "fouling." Those who study communities growing on macrophytes are more consistent. Some authors usually avoid the term "fouling" and use the more neutral terms "community" (Zavodnik 1967) or simple "peuplement" (Bellan-Santini 1964). More often, they use terms with the prefix "epi-": "epiphyton" (Makkaveeva 1979), "invertebrate epiphytes" (Hayward 1980) and "algal epifaunas" (Seed and O'Connor 1981). Reznichenko and coauthors (1976) regard all anthropogenic substrata submerged in the sea as special, differing markedly from the natural benthic and pelagic substrata. These authors believe that anthropogenic substrata with a total area greater than 2000 m² often produce a critical effect on surrounding populations and play a role in subsequent changes of all communities. This approach makes it reasonable to distinguish an independent human-induced zone, along with the zones mentioned above.

The present studies of fouling and epiphyton communities of the Seychelles Islands resulted in substantiation of the independent nature of the anthropal zone. Since the material was collected from different zones simultaneously using consistent methods, it is possible to compare the results. The degree of similarity of algal lists on different substrata was estimated using the coefficient of Serensen-Chekanovsky. A dendrogram of similarity based on the data represents a hierarchy of all possible groups of objects (Figure 1). The dendrogram shows that the objects at the level of 35% similarity can be divided into two groups: algae of epiphyton (to the left) and algae of anthropogenic substrata. It appears that substrata are united into types irrespective of the sampling area. Accordingly, the level of similarity of epiphyton algae from different areas is higher than that for fouling and epiphyton algae of the same area. The only exception is made by the species list of epiphyton algae for Mahé and Cerf Islands (object No. 10), which are separated into a special branch, probably explained by anthropogenic influences on the water of Victoria Harbor and also by the absence of *Thalassodendron ciliatum*, the usual substratum for the epiphyton on other islands.

Similar estimates of fouling and benthos similarity were made for the coastal waters of Vietnam and resulted in the same result; however the similarity of intertidal and fouling species was even lower (about 10%). Thus, the data form the basis for distinguishing anthropal substrata as an independent zone. Based on the peculiarity of communities of sessile organisms inhabiting living substrata, it would be reasonable to accept the phytocoenological term "epibioses" and "epiphyton" for plant substrata. Such a division would permit a strict discrimination of the terms "benthos" and "fouling" and eliminate their possible use as synonyms.

In spite of their qualitative diversity, fouling algae did not develop high biomass on the substrata studied. A submerged vessel near Farquhar Island represents an exception: the *Sargassum ilicifolium* biomass on its horizontal surface reached $5 \text{ kg} \cdot \text{m}^{-2}$. However, this value was also relatively low compared with the biomass of brown algal foulings recorded for boreal waters. Algal foulings with high species diversity and small biomass were characteristic of small oceanic islands (Farquhar, Aldabra, Desroches). Attached animals were represented only by *Lepas anatifera*. Similar fouling communities of the oceanic type are characteristic of long-voyage vessels and the various artificial objects drifting in open oceanic waters.

The fouling community on a pier situated in an enclosed bay on Praslin Island included approximately equal numbers of algal and animal species with a predominance of the cirripedia *Tetraclita squamosa*. The waters of Victoria Bay are subjected to considerable anthropogenic influence. Towards the inner bay, algae in fouling communities decreased in species number and were absent on steel constructions. Cirripedia and bivalves were the main components of foulings in the port, with maximum biomass of $26 \text{ kg} \cdot \text{m}^{-2}$ on pier constructions. Fouling communities on hydrotechnical constructions in Victoria Bay were dominated by the same species of bivalve molluscs (pinctads, oysters, pterias and the barnacle *Megabalanus tintinnabulum*) that were found on VIETSOVPETRO platforms in the South China Sea (Zvyagintsev, in press).

The majority of ITV's examined appeared to be unfouled, due probably to being covered with anti-fouling paints. The dominant species *Balanus reticulatus* on fouled vessels produced a mean biomass of about $26 \text{ g} \cdot \text{m}^{-2}$; these were small individuals (3 mm diameter at the shell base) and apparently did not cause enough increase in hydrodynamic resistance to critically slow vessel speed.

An analysis of the foulings on previously cleaned and untreated underwater hull surfaces of the R/V Akademik A. Nesmeyanov showed that within two weeks, cleaned quadrats were more extensively fouled than untreated control surfaces (Table 10). Further succession of fouling communities on both areas was similar. Thus, cleaning of underwater surfaces does not appear to be universally effective in tropical waters, but most likely promotes the rapid development of newly settled fouling organisms.

The massive development of some commercially valuable species in the fouling communities of vessels and hydrotechnical constructions can be considered as prospects for cultivation. To provide recommendations for the cultivation of attached forms, different anthropogenic substrata should be tested experimentally. Such experiments would be time-consuming and expensive. Fouling of a variety of anthropogenic substrata - vessels, piers, buoys, - represent natural experiments. Every object can be regarded as an "experimental plate" and the results of observations are useful for developing practical recommendations. Accordingly, our investigation of the composition and distribution of fouling organisms on hydrotechnical constructions in the Seychelles did not reveal promising prospects for the cultivation of bivalve molluscs for the majority of the study areas. Only in Victoria Harbor were bivalve molluscs found abundantly on buoy and pier constructions, but the possibility of cultivating edible organisms under anthropogenically disturbed conditions is questionable.

CONCLUSIONS

About a fourth of all algal species recorded in the Seychelles Islands as well as a majority of animal taxa were found in the fouling communities of the coastal waters. Some of the species did not occur in the natural benthos. Comparisons of the species composition between fouling and epiphyton algal associations documented the special character of anthropogenic substrata as producing an independent biotope. Epiphyton may comprise a potential source of fouling organisms since a number of common species were found on artificial substrata as well as marine plants.

Fouling of ITVs in the area under study does not present a critical problem as in boreal waters. Long-voyage vessels have somewhat heavier fouling and lose 1-1.5 knots in cruising speed after 2-3 months following cleaning. The manipulative experiment on the R/V Akademik A. Nesmeyanov showed that underwater cleaning is not effective in the long term in tropical waters.

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Table 1. Composition and distribution of fouling organisms on a submerged vessel at Farquhar Island. A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples.

Taxon	0 m		2 m		4 m	
	B	A	B	A	B	A
Algae						
<i>Struvea anastomosans</i>	650.0	-	250.0	-	175.0	-
<i>Ulva rigida</i>	52.5	-	27.5	-	14.4	-
<i>Dictyopteris delicatula</i>	10.0	-	6.2	-	10.0	-
<i>Padina minor</i>	7.5	-	1.0	-	-	-
<i>Sargassum ilicifolium</i>	-	-	-	-	4750.0	-
<i>Gelidium pusillum</i>	5.0	-	2.5	-	20.0	-
<i>Jania unguolata</i>	975.0	-	650.0	-	225.0	-
Animals						
Actiniaria	0.5	25	-	-	-	-
Nereidae	0.2	100	+	+	+	+
Sabellidae	-	-	+	+	-	-
Spirorbidae	-	-	+	+	-	-
Sipunculidae	0.5	100	0.2	25	-	-
Amphipoda	2.5	2000	0.2	125	0.5	300
Isopoda	1.0	75	0.7	75	2.5	125
Paguridae	4.0	75	-	-	-	-
Decapoda	0.2	5.0	-	-	-	-
<i>Mitrella</i> sp.	-	-	-	-	0.2	50
<i>Triphora</i> sp.	-	-	-	-	+	+
Bryozoa	-	-	+	-	-	-

Table 3. Composition and distribution of fouling organisms on a navigational buoy at Desroches. A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples.

Taxon	0 m		1 m	
	B	A	B	A
Algae				
<i>Enteromorpha clathrata</i>	420	-	21	-
<i>Enteromorpha intestinalis</i>	+	-	+	-
<i>Enteromorpha kylinii</i>	+	-	+	-
<i>Dictyota bartayresiana</i>	+	-	+	-
<i>Dictyopteris delicatula</i>	+	-	+	-
<i>Giffordia mitchellae</i>	+	-	+	-
<i>Lobophora variegata</i>	+	-	+	-
<i>Antithamnionella</i> sp.	+	-	+	-
<i>Champia parvula</i>	+	-	+	-
<i>Centroceras apiculatum</i>	+	-	+	-
<i>Centroceras clavulatum</i>	+	-	+	-
<i>Ceramium gracillimum</i>	+	-	+	-
<i>Ceramium mazatlanense</i>	+	-	+	-
<i>Ceramium</i> sp.	+	-	+	-
<i>Crouania</i> sp.	+	-	+	-
<i>Dasia mollis</i>	+	-	+	-
<i>Dictyurus prupurascens</i>	50	-	30	-
<i>Griffithsia metcalfii</i>	+	-	+	-
<i>Griffithsia subcylindrica</i>	+	-	+	-
<i>Herposiphonia tenella</i>	+	-	+	-
<i>Heterosiphonia wurdemannii</i>	+	-	+	-
<i>Heterosiphonia</i> sp.	+	-	+	-
<i>Hypnea pannosa</i>	+	-	+	-
<i>Hypnea esperi</i>	+	-	+	-
<i>Jania capillacea</i>	+	-	+	-
<i>Laurencia</i> sp.1	+	-	+	-
<i>Laurencia</i> sp.2	+	-	+	-
<i>Plocamiun</i> sp.	+	-	+	-
<i>Polysiphonia mollis</i>	380	-	400	-
<i>Peyssonelia</i> sp.	-	-	20	-
Animals				
Hydroidea	+	-	-	-
Neridae	-	-	2	200
Serpulidae	+	+	1	+
<i>Lepas anatifera</i>	670	1100	-	-
<i>Balanus reticulatus</i>	3	200	-	-
Amphipoda	3	2300	3	3000
Isopoda	+	+	-	-
Decapoda	0.2	100	-	-
<i>Mitrella</i> sp.	-	-	+	+
Ascidacea	+	+	-	-

Table 4. Composition and distribution of fouling organisms on a pier at Praslin Island. A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples. * represents sides exposed to wave action and ** denotes the protected side.

Taxon	1 m*		1 m**		2 m*		2 m**	
	B	A	B	A	B	A	B	A
Algae								
<i>Bryopsis pennata</i>	+	-	+	-	+	-	+	-
<i>Chlorodesmis comosa</i>	+	-	+	-	-	-	-	-
<i>Cladophoropsis sundanensis</i>	+	-	+	-	-	-	-	-
<i>Enteromorpha intestinalis</i>	+	-	+	-	-	-	-	-
<i>Lobophora variegata</i>	2.5	-	+	-	-	-	-	-
<i>Sargassum ilicifolium</i>	+	-	+	-	-	-	-	-
<i>Antithamnion lherminieri</i>	1	-	21	-	0.2	-	0.1	-
<i>Centroceras clavulatum</i>	+	-	+	-	-	-	-	-
<i>Ceramium gracillimum</i>	+	-	+	-	-	-	-	-
<i>Gelidiella lubrica</i>	+	-	+	-	-	-	-	-
<i>Gelidium pusillum</i>	+	-	+	-	+	-	-	-
<i>Griffithsia metcalfii</i>	+	-	+	-	+	-	-	-
<i>Gymnothanmion bipinnata</i>	1	-	23	-	0.1	-	0.1	-
<i>Hypnea esperi</i>	+	-	+	-	-	-	-	-
<i>Hypoglossum</i> sp.	+	-	+	-	-	-	-	-
<i>Jania capillacea</i>	+	-	+	-	+	-	+	-
<i>Laurencia</i> sp.1	+	-	+	-	-	-	-	-
<i>Lophocladia trichoclados</i>	+	-	+	-	+	-	-	-
<i>Fosliella farinosa</i>	+	-	+	-	-	-	-	-
<i>Peyssonnelia</i> sp.	22	-	20	-	+	-	+	-
Animals								
<i>Spongia</i>	230	-	20	-	-	-	-	-
<i>Actiniaria</i>	10	175	-	-	-	-	-	-
<i>Obelia</i> sp.	+	-	-	-	-	-	-	-
<i>Hydroidea</i>	+	-	-	-	-	-	-	-
<i>Acropora pulchra</i>	+	-	-	-	+	-	+	-
<i>Favia pallida</i>	+	-	+	-	-	-	-	-
<i>Pocillopora damicornis</i>	+	-	+	-	+	-	+	-
<i>Nereidae</i>	0.2	125	-	-	-	-	-	-
<i>Serpulidae</i>	2.5	-	-	-	-	-	-	-
<i>Sipunculidea</i>	2.5	50	-	-	-	-	-	-
<i>Tetraclita squamosa</i>	5250	600	-	-	170	75	-	-
<i>Decapoda</i> 1	+	-	+	+	-	-	-	-
<i>Decapoda</i> 2	-	-	+	+	-	-	-	-
<i>Isopoda</i>	-	-	0.5	125	-	-	-	-
<i>Druppa</i> sp.	-	-	+	-	-	-	-	-
<i>Morula</i> sp.	-	-	+	-	-	-	-	-
<i>Patella</i> sp.1	+	-	+	-	-	-	-	-
<i>Ophiuroidea</i>	1	50	-	-	-	-	-	-

Table 5. Composition and distribution of fouling organisms on an inlet buoy and chain at Victoria Harbor, Mahé. A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples.

	0 m	1 m	1.5m	2 m	3 m	5 m	10 m
Taxon	B/A	B/A	B/A	B/A	B/A	B/A	B/A
Algae							
<i>Bryopsis pennata</i>	-	-	-	-	-	-	+
<i>Derbesia marina</i>	-	-	-	-	-	-	+
<i>Feldmannian breviariculata</i>	1200	-	-	-	-	-	-
"Heterochordaria"	1300	-	-	-	-	-	-
<i>Antithamnion lherminieri</i>	-	-	-	+	-	-	-
<i>Antithamnionella</i> sp.	-	-	-	-	-	-	+
<i>Champia salicornioides</i>	-	-	-	-	-	-	+
<i>Ceramium fastigiatum</i>	-	-	-	-	+	+	+
<i>Griffithsia tenuis</i>	-	-	-	+	-	-	-
<i>Heterosiphonia wurdemannii</i>	-	-	-	+	+	-	+
<i>Lophosiphonia villum</i>	-	-	-	-	-	+	+
<i>Spermothamnion investiens</i>	-	-	-	-	+	+	+
<i>Sphacelaria furcigera</i>	-	-	-	-	-	+	-
Animals							
<i>Spongia</i>	-	-	-	20	8	2	32
<i>Actiniaria</i>	-	90/ 3200	35/ 1500	44/ 1800	+	2/ 120	1/ 120
<i>Hydroidea</i>	+	+	2	+	+	+	+
<i>Nereidae</i>	.5/300	2/1200	5/800	12/880	32/1200	120/1000	72/1400
<i>Sabellidae</i>	-	-	-	6	4	8	4
<i>Serpulidae</i>	-	-	150	8	4	+	4
<i>Sipunculidea</i>	-	-	-	4/120	-	4/80	3/160
<i>Balanus reticulatus</i>	190/800	-	-	-	-	-	-
<i>Megabalanus tintinnabulum</i>	-	14000/ 3000	9100/ 2600	3840/ 1120	7200/ 1280	7600/ 1800	19200/ 3360
<i>Amphipoda</i>	8/4000	10/4300	7/3500	4/1800	2/1200	1/800	2/1000
<i>Decapoda 1</i>	-	-	-	-	68/120	+	44/200
<i>Decapoda 2</i>	1/200	-	+	-	-	16/1600	12/160
<i>Pantopoda</i>	+	-	-	-	-	+	+
<i>Stomatopoda</i>	-	-	-	-	-	-	28/120
<i>Thais</i> sp.	-	-	-	-	-	+	-
<i>Pinctada margaritifera</i>	-	8000/ 100	-	16400/ 1600	+	2680/ 1600	+
<i>Pteria penquin</i>	-	-	+	-	-	-	-
<i>Ostrea</i> sp.	-	-	-	-	-	+	-
<i>Barbatia lima</i>	-	-	-	-	-	+	-
<i>Bryozoa</i>	-	-	200	-	-	-	-
<i>Ascidacea</i>	20	180	4500	1680	5600	9600	4800

Table 6. Composition and distribution of fouling organisms on a mooring buoy and chain at Victoria Harbor, Mahé. A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples.

Taxon	0 m B/A	1 m B/A	1.5 m B/A	2.5 m B/A	5 m B/A	10 m B/A
Algae						
<i>Ulva rigida</i>	+	-	-	-	-	-
<i>Feldmannia breviarticulata</i>	460	-	-	-	-	-
Animals						
Spongia	-	-	-	-	124	8
Hydroidea	-	-	+	+	+	4
Nereidae	-	-	6/500	140/320	14/320	32/320
Sabellidae	-	8	14	440	84	48
Serpulidae	+	-	-	+	+	+
Sipunculidea	-	-	+	-	-	-
<i>Balanus reticulatus</i>	460/ 1500	950/ 3500	1950/ 1500	2200/ 320	480/ 190	-
<i>Megabalanus tintinnabulum</i>	-	-	-	400/ 40	880/ 160	1680/ 2300
Amphipoda	1/1200	4/2500	22/11000	1/480	2/750	-
Isopoda	1/300	-	4/600	-	-	-
Decapoda 1	+	-	12/300	24/320	24/100	20/80
Decapoda 2	-	+	5/200	8/160	84/240	96/1600
Pantopoda	-	-	-	-	+	+
Stomatopoda	-	+	-	-	-	-
<i>Ostrea</i> sp.	-	1340/ 500	-	9600/ 1400	12800/ 2040	15200/ 1680
<i>Pinctada margaritifera</i>	-	-	-	-	-	+
<i>Spondylus</i> sp.	-	-	-	-	-	+
<i>Bugula</i> sp.	-	520	960	44	-	+
"Membranipora"	-	-	240	+	-	-
Acidiacea	12	190	420	960	320	720
Pisces	-	-	-	-	+	-

Table 7. Composition and distribution of fouling organisms on a pier with steel construction at Victoria Harbor, Mahé. A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples.

Taxon	0 m B/A	1 m B/A	2.5 m B/A	5 m B/A	8 m B/A
Animals					
Spongia	-	-	10	-	2000
Hydroidea	4	5	22	15	-
Nereidae	+	4/1200	80/1000	65/800	4/500
Sabellidae	-	6	20	20	15
Serpulidae	+	4	15	5	2
<i>Balanus reticulatus</i>	680/ 5500	10/ 300	6/ 200	10/ 200	10/ 200
Amphipoda	-	-	-	1/500	1/600
Decapoda 1	-	29/400	6/200	50/800	450/100
Decapoda 2	-	12/300	7/300	+	8/200
Sipunculidea	-	-	-	-	+
<i>Mitrella</i> sp.	-	+	1/300	1/300	-
<i>Ostrea</i> sp.	-	26000/ 5200	17000/ 35000	19000/ 4100	8500/ 1100
"Membranipora"	-	13	+	2	-
Ascidacea	-	20	70	55	-

Table 8. Composition and distribution of fouling organisms on an inactive dredge at Victoria Harbor, Mahé. A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples.

Taxon	0 m		2 m		4 m	
	B	A	B	A	B	A
Algae						
<i>Ulva rigida</i>	-	-	+	-	-	-
<i>Feldmannia breviarticulata</i>	-	-	620	-	-	-
<i>Acrochaetium seriatum</i>	-	-	+	-	-	-
<i>Hypnea pannosa</i>	-	-	+	-	-	-
Animals						
Hydroidea	-	-	-	-	38	-
Nereidae	+	-	8	700	2	600
Sabellidae	-	-	+	-	3	-
Serpulidae	-	-	+	-	1	-
<i>Balanus reticulatus</i>	160	1800	200	2500	130	1400
Amphipoda	-	-	8	5500	8	3000
Isopoda	2	600	-	-	+	+
Decapoda 1	-	-	-	-	5	200
Decapoda 2	-	-	-	-	1	100
Pantopoda	-	-	-	-	+	+
<i>Littorina</i> sp.	4	400	+	+	+	+
<i>Patella</i> sp.1	14	100	-	-	-	-
<i>Patella</i> sp.2	15	100	-	-	-	-
<i>Planaxis</i> sp.	36	500	-	-	-	-
<i>Trochus</i> sp.	1	200	-	-	+	-
<i>Ostrea</i> sp.	-	-	2250	800	4800	2000
Modiolus	-	-	10	300	-	-
<i>Bugula</i> sp.	-	-	18	-	-	-
Ascidacea	-	-	+	-	-	-

Table 9. Composition and distribution of fouling organisms on an operational vessel in use at Victoria Harbor, Mahé. A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples.

Taxon	0 m		2 m		4 m	
	B	A	B	A	B	A
Algae						
<i>Enteromorpha clathrata</i>	145	-	-	-	-	-
<i>Acrochaetium seriatum</i>	+	-	-	-	-	-
<i>Erythrotrichia carnea</i>	+	-	-	-	-	-
<i>Hypnea pannosa</i>	+	-	-	-	-	-
<i>Leveillea jungermannioides</i>	+	-	-	-	-	-
Animals						
Serpulidae	-	-	4	-	7	-
<i>Balanus reticulatus</i>	6	1000	18	3200	26	4200
Amphipoda	+	+	+	+	-	-
Isopoda	+	+	+	+	-	-

Table 10. Succession of fouling communities on the submerged hull of the R/V Akademik A. Nesmeyanov during the expedition (December, 1988 - March, 1989). A represents population density in individuals·m⁻². B represents biomass in g·m⁻². + indicates qualitative presence and - indicates absence in the samples. * represents values for untreated surfaces, ** denotes values for previously cleaned surfaces near the waterline.

Taxon	12/1/89		28/1/89		10/2/89		23/2/89		14/3/89	
	*	**	*	**	*	**	*	**	*	**
	B	-	B/A	B/A	B/A	B/A	B/A	B/A	B/A	B/A
Algae										
<i>Enteromorpha linza</i>	900		975	875	1550	1750	20	47	465	862
<i>Cladophora laetevirens</i>	+		.5	.1	+	+	+	+	1	1
<i>Ulva rigida</i>	-		+	+	+	+	-	-	-	-
Animals										
Serpulidae	-		+	+	+	+	2	7	1	1
Nereidae	-		-	-	+	-	+	-	-	-
<i>Lepas anatifera</i>	-		3/350	13/975	2/50	5/150	-	-	.1/125	.2/225
<i>Balanus reticulatus</i>	-		+	+	.1/200	.1/300	.5/75	.4/50	.1/250	.1/200
Amphipoda	-		+	+	-	+	+	+	-	-
Isopoda	-		-	-	-	-	-	+	-	-
Decapoda	-		+	+	-	+	-	-	-	-

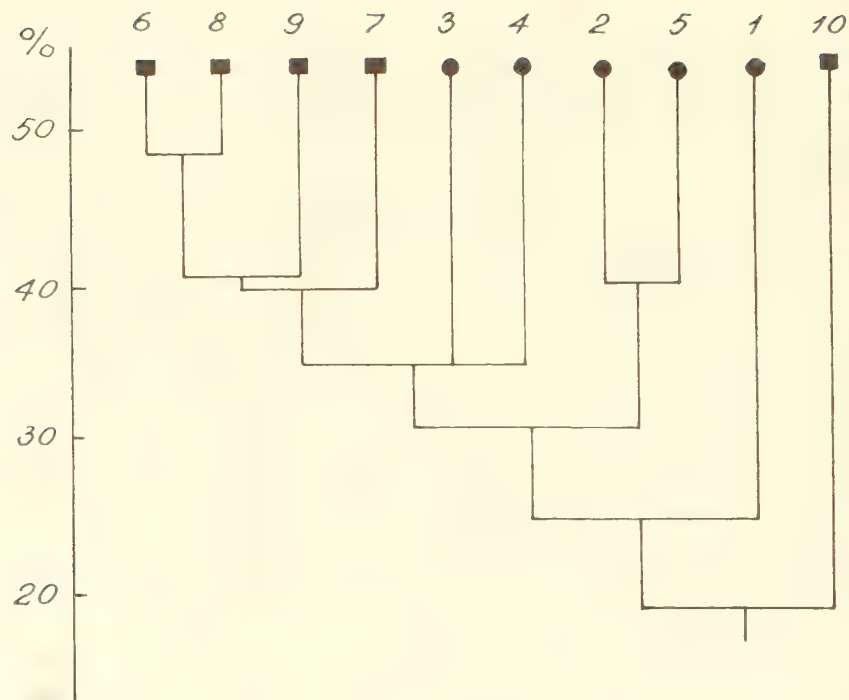


Figure 1. Dendrogram of similarity of qualitative composition of fouling algal flora (●): 1 - submerged vessel, Farquhar Is.; 2 - buoy, Aldabra Is.; 3 - buoy, Desroches Is.; 4 - pier, Praslin Is.; 5 - buoy, pier, Victoria Harbor; and epiphyton (■): 6 - Cœtivy Is.; 7 - Farquhar Is.; 8 - Aldabra Is.; 9 - Desroches Is.; 10 - Mahé, Cerf Is.

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CHAPTER 7
NITRIFICATION, DENITRIFICATION AND NITROGEN FIXATION
IN BOTTOM SEDIMENTS OF LAGOONS OF
THE SEYCHELLES ISLANDS

BY
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ABSTRACT

Major processes of the nitrogen cycle (i.e., nitrogen fixation, denitrification, ammonia mineralization and nitrification) were investigated in coastal sediments of several Seychelles Islands. Sediments were represented by carbonate sands, except in Victoria Harbor where they were carbonate silt. Nitrogen fixation was measured by acetylene reduction assay, other processes were studied by an experimental flow-through system with regulated nitrogen and oxygen concentrations. In anoxic conditions, nitrate reduction to nitrite and denitrification were determined in all sediment samples. The rates of these processes are rather low, the constants of Michaelis-Menten's equation are adduced; V_{\max} shows values ranging from $0.2-1 \mu\text{M}\cdot\text{cm}^{-3}\cdot\text{h}^{-1}$, $K_m \approx 15-30 \mu\text{M}$.

Nitrification did not occur in sandy sediments, and showed low rates ($V_{\max} \approx 0.1 \mu\text{M}\cdot\text{cm}^{-3}\cdot\text{h}^{-1}$, $K_m \approx 12-15 \mu\text{M}$) in silty sediments. Denitrification and nitrification rates were dependent on oxygen tension in silty sediments. Overall, the rates of nitrogen transformation in benthic coastal sediments of the Seychelles Islands are considerably lower than in temperate regions. It is probable that the nitrogen cycle in these coastal waters is mainly controlled by processes in very deep vs. shallow waters.

INTRODUCTION

Nitrogen and phosphorus are the most important limiting nutrients and their chemical and biological cycles significantly determine the productivity of marine ecosystems. Dinitrogen is the main component of the atmosphere and a great amount is dissolved in seawater, whereas the concentration of dissolved inorganic nitrogen compounds is usually very low. Dinitrogen is rather inert chemically and only a few bacteria and Cyanophyta can bind it in the form of ammonia during nitrogen fixation. Another process of nitrogen binding, which is less significant at an oceanographic scale, is nitrogen oxidation by atmospheric oxygen during thunderstorm electrical discharges, with products falling into the ocean via rain.

The formation of dinitrogen (to a lesser degree - nitrous oxide) from nitrogen combinations is called denitrification, with both gases being ultimately released into the atmosphere. Denitrification is a microbiological process, chiefly the result of nitrate and nitrite reduction in anoxic conditions. During nitrification, i.e., microbial oxidation of ammonia to nitrite, small amounts of nitrous oxide

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are released, especially at low oxygen concentrations. In the end, low concentrations of nitrogen compounds in seawater are the result of equilibrium between nitrogen fixation, nitrogen input from land and the atmosphere and denitrification. The natural cycle of nitrogen transformation is complex, including numerous nitrogen compounds with different valency, which can act either as oxidizers or reducers (Fig. 1).

It is generally accepted that in oxic (aerobic, oxidative) conditions nitrification mainly occurs, whereas in anoxic (reductive) conditions oxidized nitrogen forms are reduced to dinitrogen and nitrous oxide and also to ammonia (Prosser 1986, Seitzinger 1986). According to established concepts, denitrification is limited to anoxic oceanic and isolated seawaters as well as to the reductive zone of marine sediments. However, microbial strains have been isolated that can denitrify in the presence of oxygen and in oxidative environments (Robertson and Kuenen 1984). The importance and occurrence of this process in nature has not been studied.

There are different versions of the nitrogen cycle in various marine sediments: the pattern for two-layer sediments with aerobic and anaerobic zones (Vanderborght et al. 1977) and the pattern of anaerobic niche in aerobic sediments (Jørgensen 1977, Jahnke 1985) with different modifications. The experimental verification of these patterns is very difficult because of the diversity of marine sediments and the necessity to understand several intrinsic parameters of a pattern which are difficult or impossible to determine *in vitro*. Certain methodical difficulties arise while studying separate processes of the nitrogen cycle and their interactions in marine sediments. In sediment pore waters all nitrogen combinations are present in low concentrations and depending on redox potential they can be readily metabolized in opposite directions. Nitrogen has no long lived radioisotopes which makes it difficult to use radioactive indicators. *In vivo*, both of the stable isotopes N^{14} and N^{15} are found in comparable concentrations, which decreases the sensitivity of N^{14}/N^{15} methods and requires long incubations. Consequently, new technical methods for investigation of nitrogen transformations in marine sediments are needed.

We used the method of flow-through percolation of a thin layer of sediments by seawater with regulated concentrations of oxygen and various nitrogen forms (Nedwell 1982, Esteves et al. 1986). In such experiments, percolation of the solution through a given sediment substitutes for natural diffusion in sediment pore waters and eliminates methodological limitations caused by diffusion. The time of microbiological and chemical reactions between solution and sediment depends on the rate of water flow-through and is not long, in our experiments it is only several minutes. The input of oxygen and certain nitrogen combinations in the system may be either maintained constant or changed according as conditions required. The data obtained under such controlled conditions can be extrapolated to natural conditions with only great care.

METHODS AND MATERIALS

Sediments. Sediments were sampled during January-March 1989. They were collected by SCUBA diving using glass and titanium tubes (diameter - 5 cm) with rubber stoppers, and immediately delivered to the laboratory for treatment. Sediments were pushed out of the tubes by piston and pH, Es and Eh values were measured directly in the tube using glass, silversulfide and platinum electrodes, with silverchloride reference electrodes. Total hydrogen sulfide content was determined by electrode potentials and pH, using dissociation constants for hydrogen sulfide in seawater: $PK_1 = 7.01$ and $PK_2 = 13.58$. However, the values obtained should be regarded as relative ones, because K_2 values may vary considerably according to different authors' data (Morse et al. 1987). Sedimentary samples were cut into 3 cm layers and the pore waters were separated from the silt by centrifugation. Pore waters could not be separated from sand sediments either by centrifugation or by pressing, and the almost complete lack of a liquid phase made it impossible to

use electrodes, except in the surface layers. Samples of 1 cm thick surface layers were extracted by 90% acetone and concentrations of chlorophyll and pheophytin in the extracts were measured by spectrophotometer. In all the experiments, sediment samples from a 2-5 cm layer were used, which contain almost no native chlorophyll. Sediment samples from 6-12 tubes were mixed to obtain greater homogeneity.

Sediment porosity was determined by drying the samples to a constant weight at 105°C. The organic matter content was estimated by dichromate combustion at 140°C with silver sulphate. The nitrogen and phosphorus content was measured by photometer after digestion of samples by sulphur and perchloric acids (Anon. 1979). Total iron content was determined by the method of atomic absorption in the analytical laboratory of the Institute of Geology after solvation of samples in a mixture of nitric and hydrofluoric acids.

Experimental apparatus. Sediment samples consisting of 1.2-1.5 cm layers were placed in 50 cm flow-through cells (Fig. 2). Intermediate filters in the sediment (glassfiber paper Whatman GFC or special analytical dense paper Filtrack 388, DDR) prevented erosion of the sediments by uneven water flow. The cell output filtrate was optically clear and was used in spectrophotometric measurements. The flow-through system (Fig. 3) consisted of nine parallel cells with sediments and three direct control channels without cells. The flow-through system was provided by a multi-channel peristaltic pump; 12 lines of the system were divided into 3 groups, each of them had 2 cells with native sediments, a cell with sterilized sediments and a direct channel without cells to control the content of input water. Each group was used for measurements after addition of known concentrations of ammonia, nitrites and nitrates.

Because the silicone tubes of the pump and the chlorvinyl connections are permeable to oxygen, special means were used to obtain anoxic conditions. The peristaltic pump and all plastic connections were placed into a hermetic chamber filled with helium, oxygen or a mixture and the main vessel with its seawater reserve and intermediate mixing vessels were flushed with the same gas mixture. All outer connections of the apparatus were made of glass. The oxygen concentration at the output could be maintained both constant or changed together with the gas content during the experiments.

Concentrations of nitrogen combinations at the input were varied from 0-50 or 100 μM , according to a given protocol, by reserve solutions of ammonia, nitrites and nitrates supplied by an auxiliary peristaltic pump into mixing vessels with seawater. The resultant solutions with increasing concentrations (to a ratio of 1:15 with seawater) were pumped through other channels of this pump to the cell inputs of the main pump. In the experiments, seawater filtered through Millepore 0.45 μm pore size filters was used.

Processes taking place in the input part of the apparatus were simulated by a form of differential equations and solved by computer. During the preliminary computer experiments, reserve solution concentrations and mixing vessel volumes were chosen in such a way that input concentrations increased throughout the experiment according to the given task.

Measurements and stability of results. All measurements were made at 23-24°C and the flow rate in each cell was $0.14 \text{ l} \cdot \text{h}^{-1}$. Experiments were begun by washing the cells in pure seawater for 6-8 h in order to remove previous pore waters and facilitate ammonia desorption; then biogenes were added and 7-8 series of measurements were made during 12-14 h.

At a constant concentration of oxygen input, after the initial washing of ammonia, the change of ammonia, nitrate and nitrite input concentrations resulted in a new equilibrium at the output within 1-1.5 h. At a constant concentration of oxygen input, the effects remained rather constant

throughout the entire period of measurements, usually increasing after 10-12 h. However, in hyperoxic conditions using pure oxygen, the nitrification rate usually began to decrease within 6-8 h.

Sterilization. In addition to biological processes, physico-chemical effects of absorption also develop in a flow-through system. Therefore, adequate control measurements are very important. We had found beforehand that heat sterilization of sediments, sterilization by formaldehyde or other chemical methods, e.g., mercuric chloride, cause substantial changes in the organic content of sediments, which are incompatible with the chemical analyses. We used sterilization by chloroform, 5 ml of which was added into the upper part of the cell and remained in the cell during the entire experiment gradually dissolving in the flow. Under the presence of chloroform, all oxidation and reduction processes of the nitrogen cycle were inhibited, excluding reduction which was not fully inhibited. Within 6-10 h during the experiments, nitrate reduction began to develop in chloroform-sterilized cells and at the end of the experiment nitrate reduction in cells with native sediments reached 5-10%.

Blank corrections were calculated on the basis of concentration changes in sterilized cells. These corrections are small, usually in the range of 0.1-0.5 μM , but they limit the accuracy of the method while using low concentrations of organisms.

Oxidized and reduced sediment forms. Silt collected in the samples from Victoria Harbor exists in two forms. An oxidized form of nearly white color is found at the surface of sediments which remain in contact with water and air and also may be found in deeper sediment strata exposed to percolating water saturated with oxygen. A reduced form of gray color is observed in lower sediment strata under conditions of percolating anaerobic solutions. The existence of these two forms is probably related to the condition of active sediment iron which changes its valency. In a flow-through system, these two forms convert from one to another depending on the oxygen concentration in the flow, but such transformation requires at least several hours. The reduced sediments form takes up oxygen from the water and this uptake is retarded by chloroform. This may explain why anaerobic processes are supported for some time in flow-through cells during percolation of reduced sediments, even by water undersaturated in oxygen, and nitrification can be observed as well. Inertiality of sediments shows a much stronger response to changes of oxygen concentration at the input than to changes of ammonia, nitrite and nitrate concentrations that is independent of the flushing of a cell up to equilibrium with solution (Table 1). In sterilized cells, the oxidized sediment form becomes reduced very slowly in the absence of oxygen, but the reduced form becomes oxidized relatively quicker than in cells with native unsterilized sediments. Under percolation by water in equilibrium with the air, an almost complete absence of oxygen at the cell output can be observed due to the high oxygen uptake by reduced sediments. At present, it is impossible to separate the possible presence of anaerobic microzones in sediments from the possibility of reduction processes with Fe^{++} in the aerobic zone.

Nitrogen fixation rate measurements. Nitrogen fixation rate was measured by the acetylene reduction method (Stewart et al. 1967). Sediment samples were put in 125 ml vessels filled with seawater, saturated with acetylene and incubated at 23-25°C (which corresponds to the ambient temperature). To measure ethylene produced by the reduction of acetylene using gas chromatography, water was sampled by vacuumed bottles (Odintsov 1981). The theoretical ratio

$$\frac{\text{C}_2\text{H}_4}{\text{N}_2} = 3$$

was used for the calculations.

Analytical methods. The oxygen concentration in water was determined by syringe modification of the Winkler method. Glass syringes (10 ml) were connected with cell outputs. Special measurements were made to determine corrections for oxygen solubility in reagents, which may be significant at low oxygen concentrations in water. The average accuracy of the oxygen determination was $\pm 0.1 \text{ ml} \cdot \text{l}^{-1}$. Oxygen concentrations at cell inputs were on the average $0.1 \text{ ml} \cdot \text{l}^{-1}$ when the system was flushed with helium, $4.8 \text{ ml} \cdot \text{l}^{-1}$ when water in equilibrium with air was used and $14.5\text{--}16 \text{ ml} \cdot \text{l}^{-1}$ when oxygen was bubbled.

Ammonia and nitrite concentrations were determined by spectrophotometer (Anon. 1979). Nitrates were preliminarily reduced to nitrites in a capillary column with cadmium-covered copper wire. The presence of nitrites during ammonia determinations causes a decrease of the optical density of the solution. On the basis of double standard solutions of ammonia and nitrites, a corrective program was developed by computer, which permits the determination of actual ammonia concentrations as a function of apparent concentrations in the presence of nitrite. However, the accuracy of the method sharply decreases if the ammonia concentration is an order of magnitude less than the nitrite concentration. This problem hampers measurements of nitrate and nitrite reduction rates in anoxic conditions (since nitrate reduction occurs in samples).

Treatment and presentation of results. The rates of the separate processes of nitrogen compound uptake, reduction and oxidation in a flow-through system depend on the concentration and activity of certain enzymes, substrata and the resultant products, such as temperature changes and oxygen concentration. As a first approximation, we assume that the rate of the process can be calculated using the Michaelis-Menten (MM) equation:

$$V = \frac{V_{\max} S}{(K_m + S)}$$

where V_{\max} and K_m are constants of the equation, S is the substrate concentration and V is the reaction rate. Equation parameters were calculated by the least squares deviation method using an algorithm for constant deviation (Cornish-Bowden 1977). The MM equation is suitable only for reactions in homogeneous liquid media and its application for flow-through systems is an approximation. For example, if the input concentration is treated as an independent variable and it decreases in a cell, methodological deviations arise that lead to an apparent increase.

If we assume that the flow of solution through sediments in a cell is homogeneous, then the enzyme reaction can be treated as a time-dependent process in homogeneous sediments and can be described using the integral form of the MM equation:

$$T = R^2 \cdot HP/V \quad V_{\max} \cdot T = S_0 - S + K_m \cdot \ln(S_0/S)$$

where R is the cell radius, H is the thickness of the sediment layer, P is the porosity, V is the flow rate; S_0 is the input substrate (or product) concentration and S is the output substrate (or product) concentration. Linear anamorphosis of this equation (Cornish-Bowden 1979) was used in the calculation of equation parameters using measurements in the flow-through system. The V_{\max} values obtained did not differ statistically from those calculated using the usual form of the MM equation, but K values were significantly lower (2-3 times). Unfortunately, the integral form can be used without significant complications only for a single product release or substrate uptake. If the substrate converts into several products, the usual form of the MM equation is employed, which should be regarded as method of experimental data presentation without reference to the process mechanisms. Tables 1-7 present values obtained with the usual form of the MM equation.

RESULTS AND DISCUSSION

Sediments. Sediments collected around low calcareous atolls are rather similar (Tables 2 and 3). They are mostly light carbonate sands without macrofauna or indications of bioturbation. Natural chlorophyll concentrations are very low (sediments from Cœtivy Atoll not included). Except in samples from Desroches Island, the hydrogen sulfide is present as detected by odor and sulfide electrode measurements. Oxic or suboxic conditions are characteristic of surface layers; lower sediment strata are slightly reduced. It should be noted that redox measurements in the presence of hydrogen sulfide are unreliable, because the platinum electrode is very sensitive to minute traces of H_2S .

Sediment samples collected off the high granitic island of Mahé in Victoria Harbor are fine carbonate silts with a small admixture of terrigenous materials. They are similar to sand sediments in terms of their general chemical composition, redox potential and pH values, but they differ by having a greater dispersion and higher iron concentration. At 12-15 cm in depth, silt sediments are followed by a sand layer which is similar to that sampled on atolls. Pore waters were centrifuged from the silt sediments, but they were minimal. These pore waters contain ammonia and orthophosphate, which increase in concentration with depth, as well as low concentrations of nitrites and nitrates (Table 4).

Ammonia mineralization. Ammonia mineralization was noted in anoxic conditions in all sediment samples of the flow-through system, although it was not very intensive (Table 5). The given values refer only to microbial production of ammonia inhibited by chloroform, since ammonia evolution also occurs in sterilized samples for a long time at very low rates, related to desorption from surfaces of sediment fractions. However, the values of biological ammonification were obtained during sediment percolation by seawater without ammonia; e.g., its evolution rate decreases with increased ammonia concentration at the input, and at concentrations of 50-100 μM , its production ceases, or in some samples, a slight uptake occurs. In anoxic conditions, very low ammonia uptake at the lower concentrations was observed only in sediments from Desroches Island (Table 5). Ammonia concentration was not measured in the pore waters of sand sediments, so the ammonification rates obtained by sediment percolation of seawater without ammonia cannot be applied to the natural conditions. In oxic silt samples, ammonia mineralization does not occur and ammonia uptake takes place due to the nitrogen fixation process. In sand, in the presence of oxygen, this process was not observed.

Nitrate reduction and nitrite and nitrate denitrification. In anoxic conditions, all sediment samples show the uptake of nitrites and nitrates and the dependence of such process rates on input concentration can be described by the MM equation (Table 5). In all cases, nitrate reduction occurs, apparently partially induced by the presence of nitrate, which is why K_m values for nitrate reduction in most cases are higher than those for nitrate and nitrite uptake. The ratio of nitrates reduced into nitrites to nitrate uptake increases from trace amounts at nitrite input concentrations as low as 4 μM to one-third at 30 μM . This finding conforms to the assumption that nitrate and nitrite uptake represents denitrification. Application of the integral MM equation shows that the K_m values, given in Tables 1-7, are 2-2.5 times higher than the actual values, i.e., maximum process rates are reached at low concentrations (from one to several tens of micromoles). That is why the maximum rates possible for denitrification processes are low and the sensitivity of methods available for estimation of molecular nitrogen and nitrous oxide are not sufficient for direct measurements of denitrification.

In the silt sediments of Victoria Harbor, the intensity of denitrification is higher than in the sandy sediments, despite similar concentrations of organic matter. This is probably due to greater quantities of bacteria in the more dispersed sediments. When water with oxygen levels in

equilibrium with air is used at a flow-through system input, nitrate reduction only occurs in traces and nitrate and nitrite uptake rates are sharply decreased. Hyperoxic conditions lead to a complete cessation of ammonification and reduction processes of the nitrogen cycle.

Nitrification. The sand sediments from low coral atolls do not take up ammonia and do not oxidize it into nitrite (or nitrite into nitrate) irrespective of the oxygen concentrations of the input water, i.e., no nitrification processes can be found. Such sandy sediments are different from those of temperate regions, where nitrification processes are common and may be found during all seasons (Wollast 1981, Kaplan 1983). Sandy sediments off the Vietnamese coasts also are characterized by significant rates of nitrification (Propp et al. 1988). Similarly, the silt sediments of Victoria Harbor are characterized by appreciable (though low) rates of nitrification processes (Table 6), which are suppressed in hyperoxic environments. At present there is no simple explanation of these differences. Several factors may be involved: e.g., bacterial numbers are usually greater in silts than in sands, there is approximately double the iron content in silts that can either regulate the redox potentials of sediments or be a component of nitrification and respiration enzymes and, lastly, it is possible that ammonia concentrations are higher in pore waters of silt sediments. Despite the low rates of nitrification in silt sediments, practically all of the ammonia evolved during ammonification can be oxidized to nitrites and nitrates at the sediment surface layer.

Nitrogen fixation. Nitrogen fixation was found in all samples investigated and fixation intensity drops sharply in deeper sediment layers (Table 7). However, the rate of nitrogen fixation possible is rather low, e.g., 1-3 times lower than the possible rate of ammonification. These values are close to those measured earlier in sand and silt sediments of coastal waters off Vietnam (Propp et al. 1988). Extremely low rates of nitrogen fixation were found in sandy sediments of the *Thalassodendron ciliatum* community near African Banks (Table 7) in the present study. The same levels of nitrogen fixation were found for pure sandy sediments off the Vietnamese coast where the organic matter content was less than 0.2%. Because of its low intensity, nitrogen fixation in sediments can compensate for nitrogen losses during ammonification and due to diffusion of ammonia only to a very limited degree.

Sediments in nitrogen balance in coastal waters of the Seychelles Islands. The extremely low concentrations of natural chlorophyll in surface layers of sandy and silty sediments shows that the photosynthetic intensity of benthic microalgae at the bottom-water interface is very low, at least during the period of investigation (in spring 1989). Destruction of organic matter in sediments prevailed though it also was not intensive, probably related to the small amount of organic matter at sediment surfaces and on its low concentration in all sediments.

Both the sandy sediments of atolls and the silt sediments of Mahé Island, Victoria Harbor, are the major sources of ammonia that is produced during ammonification in the anaerobic layer of sediments. Production of organic nitrogen combinations due to nitrogen fixation is considerably smaller (1-3 times). Since nitrification in sandy sediments of the carbonate atolls is not prevalent, ammonia is not converted into nitrogen due to denitrification. Sediments can denitrify only small quantities of nitrates from the bottom-water boundary layer because the nitrate concentration in this layer is very low and the gradient between the bottom layer waters and the sediment pore waters may be quite small.

Nitrate and nitrite concentrations in the pore waters of silt sediments of Victoria Harbor were somewhat higher. These two nitrogen forms may be partially denitrified both by diffusion into sediment anaerobic zones and due to denitrification during suboxic and aerobic conditions. Processes in such sediments represent mechanisms of molecular nitrogen formation from its various compounds, but their intensity is low due to small concentrations of nitrate and nitrite in both bottom and pore waters. As a whole, the role of sediments in the nitrogen cycle, as a possible

regulator of the overall total supply, is not predominant because of low rates of nitrogen transformation. In the reef ecosystems of the Seychelles Islands, nitrogen cycle processes in very deep waters are probably more important.

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Table 1. Rates of nitrate and nitrite uptake, nitrate ammonification and nitrification in a flow-through system at different oxygen input levels ($\text{ml}\cdot\text{l}^{-1}$). The difference of nutrient input/output concentrations, μM ; Victoria Harbor silt was initially in reduced form; NH_4 , NO_2 , NO_3 input concentration was $20\mu\text{M}$.

Step	O_2 conc. $\text{ml}\cdot\text{l}^{-1}$		Uptake		Nitrate-reduction $\text{NO}_3^- \rightarrow \text{NO}_2^-$	Nitrate ammonification $\text{NO}_3^- \rightarrow \text{NH}_4^+$	Nitrification	
	input	output	NO_2^-	NO_3^-			$\text{NH}_4^+ \rightarrow \text{NO}_2^-$	$\text{NH}_4^+ \rightarrow \text{NO}_3^-$
1	0.3	0.1	-10.5	-10.8	2.05	1.13	0	0
2	0.3	0.1	-10.2	-9.9	2.03	0.8	0	0
3	2.02	0.1	-6.2	-7.5	1.18	0	0	0
4	1.9	0.3	-5.2	-6.8	1.1	0	0	0
5	4.8	0.6	-1.8	-6.0	0.6	0	0.3	0.21
6	4.6	0.9	-1.2	-5.8	0.5	0	0.17	0.30
7	15	9.0	-1.0	-4.5	0	0	0.48	0.58
8	15	11.0	-0.5	-4.0	0.05	0	0.47	0.61

Table 2. Common features and photosynthetic pigment contents of sediments (number of measurements given in parentheses).

Locality	Depth m	Porosity %	Content, % of dry wt.			Total Fe	Pigments, $\text{mg}\cdot\text{m}^{-2}$	
			$\text{C}_{\text{org.}}$	N	P		chlorophyll a	pheophytin a
Cœtivy	26	61/12/	0.46/2/	0.046/2/	0.04/2/	$0.154 \pm 0.016(3)$	$47 \pm 10/4/$	$67 \pm 11/4/$
Desroches	27	67/12/	0.40/1/	0.037/1/	0.08/1/	$0.2 \pm 0.01(2)$	$3.5 \pm 1.5/5/$	$5 \pm 1/5/$
St. Joseph	3	49/8/	0.40/1/	0.04/1/	0.084/1/	$0.15 \pm 0.018(4)$	$0.23/2/$	$0.36/2/$
Mahé, Victoria Harbor	14	45/12/	0.42/4/	0.035/5/	0.032/5/	$0.245 \pm 0.014(10)$	$1/2/$	$11/2/$

Table 3. Redox potential (corrected for nitrogen electrode), total H₂S content in pore water, μ M; pH in sediments.

Layer cm	Cœtivy			Desroches			St. Joseph			Mahé		
	Eh	H ₂ S	pH	Eh	H ₂ S	pH	Eh	H ₂ S	pH	Eh	H ₂ S	pH
0-3	-43	0.07	7.76	87	0	7.7	225	-185	-	99	-720	7.62
3-6	-48	21	7.64	-3	-0.6	7.68	130	-210	-	13	-19	7.40
6-9	-33	36	7.59	-13	-9	-	90	-238	-	-6	-30	7.63
9-12	-53	-22	7.49	-33	-14	-	70	-369	-	27	-15	7.60
12-15	-53	155	-	-	-	-	70	-343	-	-	-	-
15-18	-63	-155	-	-	-	-	60	-380	-	-	-	-
18-21	-33	150	-	-	-	-	60	-	-	-	-	-

Table 4. Nutrient (PO₄, NH₄, NO₂, NO₃) concentrations, μ M, in bottom and pore waters of Victoria Harbor sediments.

	PO ₄	NH ₄	NO ₂	NO ₃
bottom waters	0.52	7.3	0.29	0.93
pore waters, 0-3cm	12.4	108	0.7	0.83
pore waters, 3-6cm	15.8	148	-	-

Table 5. MM equation parameters for processes of nitrogen reduction in anoxic conditions in Seychelles Island sediments (ammonia mineralization - $\mu\text{M}\cdot\text{cm}^{-3}\cdot\text{h}^{-1}$; numerator - V_{max} , $\mu\text{M}\cdot\text{cm}^{-3}\cdot\text{h}^{-1}$; denominator - K_m , μM ; in parenthesis - number of measurements)

Processes	Cœtivy	Desroches	St. Joseph	Mahé
Ammonia mineralization	$0.08 \pm 0.008/6/$	$0.02 \pm 0.03/6/$	$0.02 \pm 0.003/6/$	$0.055 \pm 0.01/6/6/$
Uptake of NH_4	0	$0.1/0.571/10/$	0	0
Uptake of NO_3	$0.436/9.93/6/$	$0.398/12.8/14/$	$0.551/20.3/14/$	$0.946/13.6/12/$
Uptake of NO_2	$-15/8/$	$0.281/6.1/14/$	$0.37/14.5/14/$	$1.23/19.5/12/$
Nitrate-reduction $\text{NO}_3 \rightarrow \text{NO}_2$	$0.16/7.73/10/$	$0.227/29.1/14/$	$0.337/69.5/14/$	$0.46/104/8/8$

Table 6. MM equation parameters for ammonia uptake and nitrification in Victoria silt sediments (numerator - V_{max} , $\mu\text{M}\cdot\text{cm}^{-3}\cdot\text{h}^{-1}$; denominator - K_m , μM ; NMM - not MM kinetics + traces of a process; 14 measurements).

Conditions	Uptake			Oxidation		
	NH_4	NO_2	NO_3	$\text{NH}_4 \rightarrow \text{NO}_2$	$\text{NH}_4 \rightarrow \text{NO}_3$	$\text{NO}_2 \rightarrow \text{NO}_3$
Normoxic	$0.814/10.8$	$0.347/54.6$	$0.246/3.5$	$0.08/12.6$	$0.104/15.4$	+
Hyperoxic	$0.22/1.53$	$0.216/1.7$	-	$0.02/-0.2$ NMM	$0.03/-0.6$ NMM	+

Table 7. Nitrogen fixation rates in some sediment samples.

Locality	Sediment	Depth, m	Layer, cm	Nitrogen fixation rate
Desroches	sand	27	0 - 3	$0.16 \pm 0.06(7)$
			4 - 7	$0.09 \pm 0.02(7)$
			8 - 11	$0.08 \pm 0.02(7)$
African Banks	sand	11	0 - 10	$0.02 \pm 0.02(13)$
			0 - 3	$0.202 \pm 0.016(5)$
			3 - 6	$0.090 \pm 0.004(3)$
Mahé	silt	14	6 - 9	$0.038 \pm 0.001(3)$
			8 - 12	$0.004 \pm 0.000(3)$
			12 - 15	$0.002 \pm 0.002(3)$

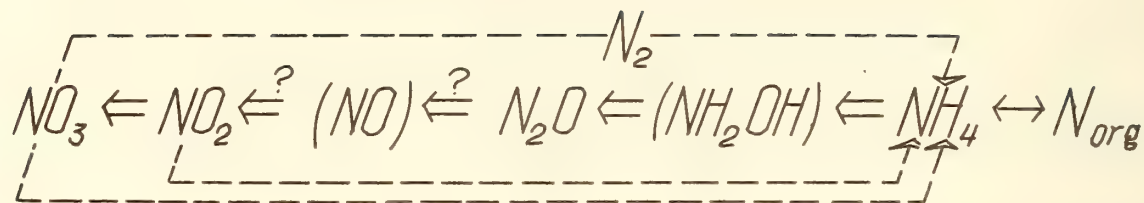


Fig. 1. Nitrogen cycle; in parentheses - nitric oxide and hydroxylamine, which probably are converted in a cell without significant release to the water; continuous line indicates processes with constant nitrogen valency; dotted line - reduction; double line - oxidation.

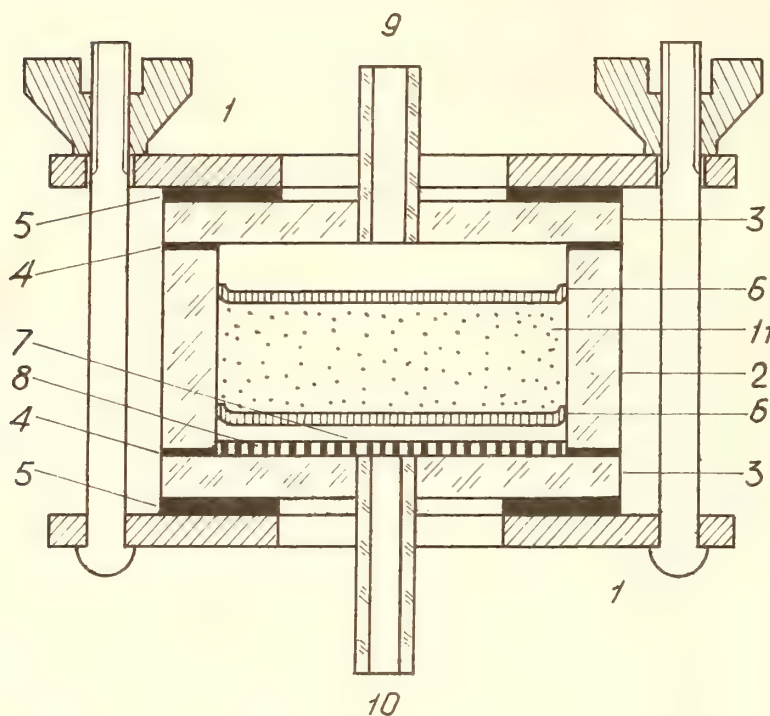


Fig. 2. Flow-through cell; 1 - compression casing; 2 - glass cylinder; 3 - glass lids; 4 - hermetic stoppers; 5 - rubber stoppers; 6 - filters; 7 - porous teflon lining; 8 - nylon net; 9 - solution input; 10 - solution output.

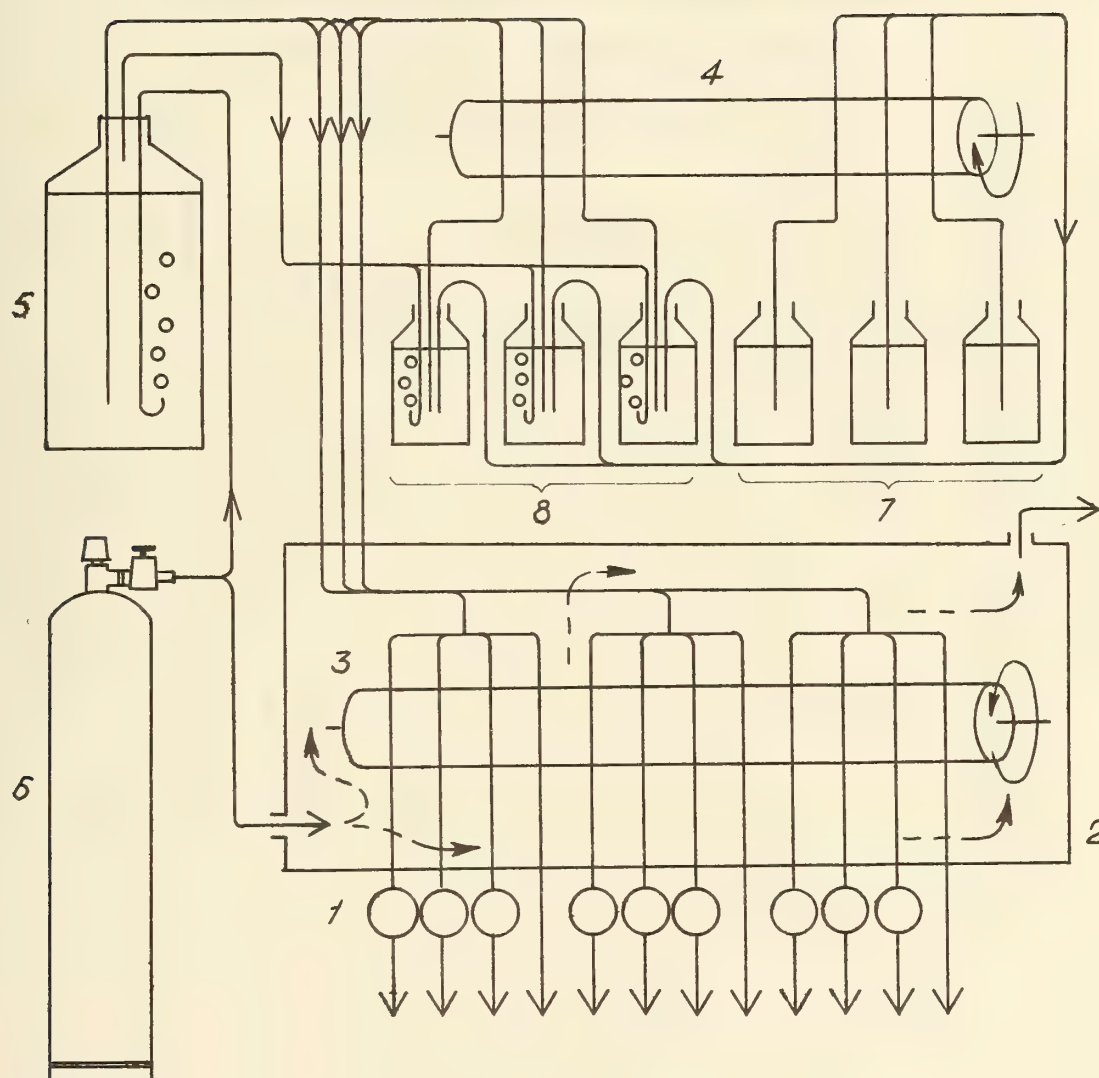


Fig. 3. Flow-through experimental system. 1 - flow-through cells; 2 - metal-glass casing; 3 - main peristaltic pump; 4 - auxiliary peristaltic pump; 5 - main seawater supply; 6 - oxygen or helium tank; 7 - nutrient supply solution bottles; 8 - intermediate mixing vessels.

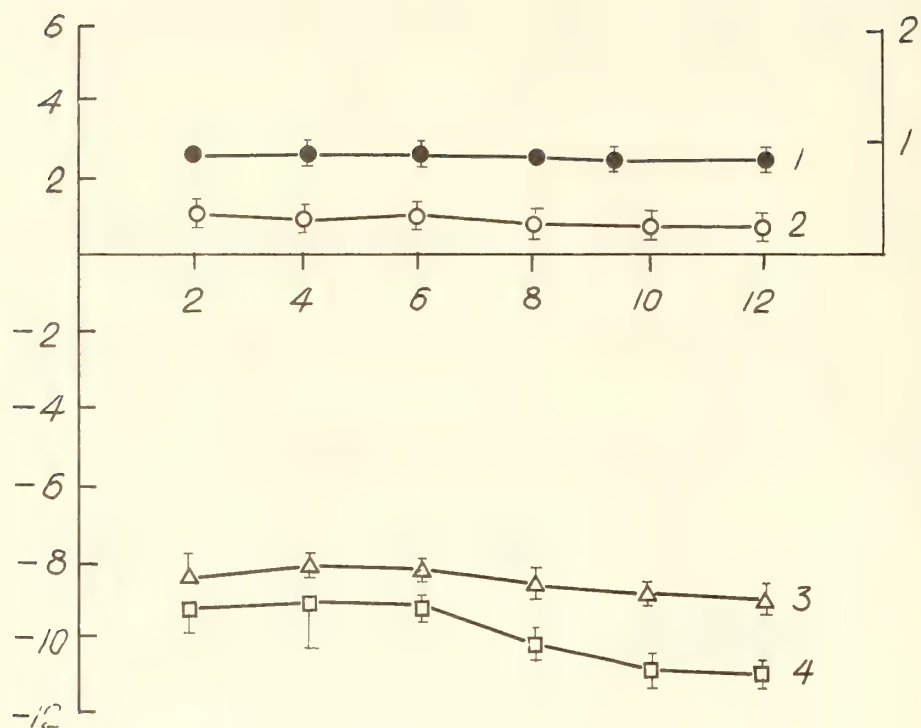


Fig. 4. The dynamics of nitrate and nitrite uptake rates and nitrate reduction at a stable biotic content ($20 \mu\text{M}$) and oxygen concentration ($0.1 \text{ ml} \cdot \text{l}^{-1}$) at flow-through system input (μM); horizontally - period from biotic addition (h).

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**CHAPTER 8
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SEYCHELLES ISLANDS
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CHAPTER 8

NITROGEN FIXING ACTIVITY ASSOCIATED WITH

SUBTIDAL MACROPHYTES OF THE

SEYCHELLES ISLANDS

BY

V.S. Odintsov *

INTRODUCTION

The ability of microorganisms to fix dinitrogen has significance for the functioning of marine offshore ecosystems in oligotrophic oceanic regions. The most effective utilization of fixed nitrogen occurs in associations of nitrogen-fixing microorganisms with macrophytes where direct contact is present. There are many examples (e.g., Harlin and Craigie 1975, Wetzel and Penhale 1979) of intensive exchange of nitrogen, phosphorus and carbon between epiphytes and their host macrophytes. It is known (Jones and Stewart 1969) that macrophytes consume fixed nitrogen released by nitrogen-fixing epiphytes. In some macrophyte communities, the correlation between productivity and epiphytic nitrogen fixation has been shown (Capone et al. 1979). Epiphytic nitrogen fixing activity associated with brown algae such as *Sargassum* may be so high that 40% of the nitrogen requirements of the algae can be met by such nitrogen fixation, assuming that all of the fixed nitrogen is consumed (Carpenter 1972, Hanson 1977, Odintsov and Lapteva 1984, Odintsov 1988).

The objective of this work was to determine the significance of nitrogen-fixing epiphytes on subtidal seagrasses and seaweeds of the Seychelles Islands in regard to their role in providing island ecosystems with nitrogen nutrients.

METHODS AND MATERIALS

Abundant macrophytes such as *Thalassodendron ciliatum*, *Sargassum cristaefolium*, *Sargassum microcystum*, *Halimeda gracilis*, as well as the more uncommon algae *Caulerpa brachypus*, *Padina* sp., *Turbinaria ornata* and *Lobophora variegata*, were used in the experiments. Nitrogen fixing activity of epiphytes was determined by the acetylene reduction method (Stewart et al. 1967), except the samples were incubated without a gas phase and sampling for gas chromatography was done with evacuated vials (Odintsov 1981). The samples were incubated in natural light. During one experiment, half of the *Sargassum* samples were washed to remove epiphytes and determine the nitrogen fixation role of symbionts living inside the thalli, the other half were used to compare the levels of the more common epiphytic nitrogen fixation. Following the experiments, portions of the samples incubated were fixed for electron microscopic study.

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RESULTS AND DISCUSSION

The levels of nitrogen fixing activities associated with Seychelles subtidal macrophytes are presented in Table 1. Negligible nitrogen fixation was detected in the samples of *Thalassodendron ciliatum* and *Lobophora variegata* collected near Desroches Island, as well as in samples of *T. ciliatum* from C  etivy Island (depth 26 m) and in samples of *Turbinaria ornata* incubated in the dark. Great differences in nitrogen fixation rates were observed in all other samples. The greatest activity was shown in specimens of *Sargassum cristaefolium* from Praslin Island and *Padina* sp., which was approximately the same as that shown by *Thalassia testudinum* and *Zostera marina* populations from temperate waters (Capone and Taylor 1979, Odintsov and Lapteva 1984). The rate of nitrogen fixation of the seagrass *T. ciliatum* was higher than that of pelagic *Sargassum* (Carpenter 1972, Hanson 1979) but lower than the rates recorded for temperate seagrasses. Therefore, populations of *T. ciliatum* do not appear to serve as an important nitrogen nutrient source for surrounding areas. Conversely, communities of *S. cristaefolium* with high biomass (Table 1) can show considerable N-fixation, similar to that of *Sargassum ilicifolium*, *S. polycistum* and *S. feldmannii* from the Thou Island area in the South China Sea (Odintsov 1988). Nitrogen fixing activity in a *Sargassum microcystum* community was comparable to that of temperate seagrasses having smaller biomass. Epiphytic nitrogen fixation in *Padina* sp. was high, but probably is important only for the host plant, because *Padina* sp. does not form communities. The same can be said concerning nitrogen fixation associated with *Turbinaria ornata*, *Halimeda gracilis* and *Caulerpa brachypus*.

Statistically significant decreases of nitrogen fixing activity in the dark was noted only in *Sargassum cristaefolium* from Praslin Island and *Padina* sp., in which photosynthetic nitrogen fixing epiphytes appear to be predominant. Nitrogen fixing epiphytes of *S. cristaefolium* are present in lightly washed mucous extracts and are not firmly attached to thalli. The exact location of such epiphytes awaits further electron microscopy study. It may be concluded that only *Sargassum* communities serve as important sources of nitrogen nutrients for surrounding ecosystems.

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Table 1. Epiphytic nitrogen fixation associated with macrophytes of the Seychelles Islands. * = values for dry weight; ** = data based on average fresh biomass of macrophytes in a community; *** = data based on average fresh biomass of macrophytes not forming community.

Species Place, Date	Depth(m)	Light	Nitrogen fixation		Number of measurments
			ng N ₂ ·g ⁻¹ ·h ⁻¹ *	mg N ₂ ·g ⁻¹ ·day ⁻¹ **	
<i>Thalassodendron ciliatum</i>					
Cœtivy, 17 Jan 89	3	+	5.6±7.0	0.5	3
	3	-	8.4± -0.1	0.75	3
	6	+	4.2±1.4	0.38	3
	6	-	21.8±10.9	2.47	3
	11	+	3.64±4.48	0.33	3
	11	-	3.36±1.96	0.30	3
	26	+	0	0	3
	26	-	13.1±162	1.18	3
<i>Sargassum cristaefolum</i>					
Praslin, 13 Feb 89	washed				
	2	+	368±128	9.85	10
	2	-	13.4±3.08	2.14	6
	unwashed				
	2	+	2017±259	63.5	9
2	-	53.5±13.4	0.97	7	
<i>Sargassum microcystum</i>					
Mahé, 17 Feb 89	1	+	255±70	3.75	10
	1	-	624±262	9.05	6
<i>Sargassum cristaefolum</i>					
Mahé, 17 Feb 89	1	+	2.24±6.72	0.03	3
	1	-	13.7±8.12	0.20	4
<i>Turbinaria ornata</i> ***					
Mahé, 17 Feb 89	1	+	0.28±1.4	0	6
	1	-	0	0	4
<i>Padina</i> sp.***					
Mahé, 17 Feb 89	0.5	+	2678±238	0	10
	0.5	-	12.0±5.04	0	4
<i>Halimeda gracilis gracilis</i>					
Cosmoledo, 9 Mar 89	5	+	15.3±4.14	0.32	9
<i>Caulerpa brachypus</i>					
Cosmoledo, 9 Mar 89	5	+	46.8±9.24	0	9

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CHAPTER 9
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CHAPTER 9

PHOTOSYNTHESIS IN COMMON MACROPHYTE SPECIES IN THE INTERTIDAL AND UPPER SUBTIDAL ZONES OF THE SEYCHELLES ISLANDS

BY

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ABSTRACT

Photosynthetic capacity, light curves of CO₂ assimilation and the path of carbon in photosynthesis of common marine macroalgae and seagrasses of the Seychelles Islands were studied by the radiocarbon method. Intertidal and upper subtidal species of marine plants have similar photosynthetic capacities but the latter decrease considerably in species growing below 25 m when the photosynthetically active radiation (PAR) is less than 15% of incident surface PAR (PAR_s). All macrophytes studied exhibited daily variations in the photosynthetic light curves. Photosynthetic light saturation values (I_k) and the angle of the initial slopes (α) of light curves increase from morning to midday and decrease again towards evening. During the evening, photosynthesis in intertidal macroalgae and seagrass was inhibited considerably by PAR greater than 250 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. When tropical species of marine plants became adapted to lower light intensities at great depths or in shaded habitats, the chlorophyll and phycoerythrin contents increased as did the efficiency of the use of low light ($<60 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Some species increased their photosynthetic capacity when shaded. Tropical seagrasses exhibited the same adaptive reaction to light as seaweeds; however, the range of variation in the structure and function of their photosynthetic apparatus was narrower than in algae.

INTRODUCTION

Our knowledge of photosynthetic productivity of benthic seaweeds and seagrasses of the tropical zone lags significantly behind the knowledge for temperate waters (Lüning 1985). Recently, Mark and Diane Littler, with coworkers, published a series of reviews and experimental papers devoted to the study of primary production and factors that control it in macroalgae of subtropical and tropical latitudes, and thus accelerated knowledge in this field of research (Littler 1973a, b, 1980, Littler et al. 1983, 1986, 1988, Littler, Kauker 1984, Jensen et al. 1985, Lapointe et al. 1987). These authors standardized the procedure of measuring the primary production of macroalgae (Littler 1979, Littler and Arnold 1985) and used this parameter for analyzing numerous species and morphological forms of algae from a wide range of environments on subtropical and tropical shores, mainly on tropical reefs in the Atlantic Ocean (Littler et al. 1983, 1986, 1988, Littler and Littler 1984, 1988, Jensen et al. 1985, Lapointe et al. 1987) and the warm temperate Pacific Ocean (Littler and Arnold 1980, 1982, Littler and Littler 1980). These and other authors (Buesa 1977, Dawes et al. 1987, Bach 1979,

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Duraco and Dawes 1980, Davis and Dawes 1981, de Ruyter van Steveninck and Breeman 1981, O'Neal and Prince 1982) demonstrated considerable fluctuations in the primary production of tropical macrophytes. The primary net production of individual macrophytes on a coral reef ranges from 0.03 to 14 mg C fixed·g dry wt⁻¹·h⁻¹, or 0.6 to 15 mg C fixed·g ash-free dry wt⁻¹·h⁻¹ (Littler and Kauker 1984, Jensen et al. 1985, Lapointe et al. 1987, Littler et al. 1988).

The net algal production in the tropics depends both on the internal conditions of the plants, which determine their productive capacity, and on external environmental factors. The most significant internal factors are seasonal variability of plants (algae have a 7-fold season-dependent difference in their production, Littler et al. 1979, Littler and Arnold 1980, O'Neal and Prince 1982), the age of thalli or their parts (Chapman 1962, Littler and Arnold 1980, Littler and Kauker 1984), reproductive status of thalli (Littler and Arnold 1980) and the existence of different growth forms (such as fine filamentous thalli, massive and crustose forms, Peterson 1972, Littler and Arnold 1980, Littler and Kauker 1984, Littler et al. 1988). Important external factors include high temperatures and desiccation of intertidal macroalgae (Littler and Arnold 1980, Mathieson and Dawes 1986), chemical characteristics of waters, (Lapointe et al. 1987, Littler et al. 1988), and irradiance (Peterson 1972, Littler and Arnold 1980).

The multidisciplinary Soviet-American expedition, aimed at the study of seaweeds and seagrasses of the Seychelles Islands, provided an opportunity to widen our knowledge of the productivity physiology of tropical macrophytes. We established two objectives:

1. To conduct research on mechanisms of adaptation of marine plants to light intensity in tropical conditions and to elucidate their dependence on the light factor and selected morpho-functional features of plants.
2. To determine the photosynthetic capacity of the most common macrophyte species and growth forms of the intertidal and upper subtidal zones of tropical island shelves.

STUDY AREAS

The capacity and photosynthetic function in marine plants inhabiting tropical environments was studied on islands of the Seychelles and Amirantes Groups: Cœtivy, Farquhar, Aldabra, Desroches, Providence, African Banks, Saint-Joseph, Cosmoledo, Astove and Praslin. Plant material was collected at depths of 0 to 50 m under different conditions of irradiance, temperature, water motion and sedimentation (Table 1).

Seaweeds and seagrasses of the intertidal zone of Aldabra, Cosmoledo and Cœtivy were subjected to stressful environments: e.g., growing mainly in intertidal pools or in dense mats on boulders and dead corals. Intertidal pools warmed to 35-37°C during the sunny midday period and algae on the mat surface received about 1200-1400 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR. Typical pools had somewhat increased salinity (to 34.9 ppt), the pH reached 8.75 ± 0.15 , the PO_4 content was 0.46 ± 0.05 ; P_{org} , 0.10 ± 0.03 ; NO_2^- , 0.34 ± 0.15 ; NH_4^+ , 1.64 ± 0.81 ; NO_3^- , 2.95 ± 1.76 ; N_{org} , 19.2 ± 3.33 μM (Novozhilov et al. 1989).

In the subtidal zone, the photon flux density (PFD) was less intensive. At the depth range of 30 to 40 m, PFD averaged 8-12% PAR_s , which in the middle of a sunny day ranged from 60-90 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Between depths of 2 to 12 m, we observed a considerable precipitation of coral sand and silt. Water temperature decreased gradually from 28°C at the surface to 26°C at 30 m deep. At a depth of 40 to 50 m, temperatures were lower (23-25°C) and only on Cœtivy did temperatures fall to 17-20°C at 40 m depth (Novozhilov et al. 1989). The content of dissolved nutrients in the bottom portion of

the upper subtidal zone (down to 30-40 m deep) differed little from that in the surface water layer, but values were much lower than in intertidal pools and had the following average values for all the islands: PO_4^{---} , 0.225 ± 0.119 ; P_{org} , 0.226 ± 0.178 ; NO_2^- , in traces; NH_4^+ , 0.35 ± 0.12 ; NO_3^- , 0.46 ± 0.37 ; N_{org} , $10.2 \pm 3.5 \mu\text{M}$. An increased content of inorganic phosphorus, PO_4^{---} , $0.45 \pm 0.08 \mu\text{M}$ was found near Cöetivy and Farquhar Is. deeper than 40 m (Novozhilov et al. 1989).

In the subtidal zone, above 20 m, macroalgae often grew among the seagrass *Thalassodendron ciliatum* and at the base of old corals. Sometimes they formed compact mats on dead corals. This means that at intermediate depths, as in the intertidal zone, marine plant communities experience a strong self-shading. At 35 m, some algae occurred as epiphytes on stalks and leaves of *T. ciliatum*, or attached to coral pebbles on sites devoid of seagrass. *T. ciliatum* did not form a continuous carpet at 33 m, but was scattered. Deeper than 35 m, seagrass beds were reduced or absent and algae colonized coral pebbles as sparse beds or individuals not shading each other.

METHODS AND MATERIALS

To analyze the productive capabilities of algae and to study their photosynthesis, we attempted to select samples not shaded by other plants. Algal shading or self-shading is shown in Table 1 in average PAR values, received by plants in their habitats. We collected plants irrespective of "life forms", Table 1 gives qualitative characteristics of the habits and the thickness of algal thalli.

When sampled from the bottom, the plants were placed (still underwater) in semi-transparent vessels and brought to the ship within 1-2 hours where they were transferred into aquaria with running seawater, biological filtering and intensive air bubbling (Butorin et al. 1980). The amount of the incident solar radiation was controlled by neutral filters made of white linen. The plants remained in the aquaria, until the next day when they were analyzed. Plants selected for analysis appeared healthy and pigmentation was typical of their natural habitat. Small plants (3-4 cm long) were measured whole, but only the middle part was taken from larger macrophytes. In *Thalassodendron ciliatum*, we analyzed mature leaves (the 2nd and the 3rd outward from the young central leaf). Prior to analysis, the plants, still underwater, were carefully freed of epiphytes under a dissection microscope and washed in fresh filtered seawater.

In situ measurements of photosynthetically active radiation.

For underwater measurements of PAR we used an autonomous irradiance meter with a photodiode of linear performance within a broad light range. In front of the photodiode a 300-740 μm -pass range compound light filter was installed to measure PAR. The limits of photon flux density measurement were within 0.24 to 3800 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The extent of PAR attenuation within the water column was measured throughout the depth range (Titlyanov et al. 1988).

A surface irradiance meter (Yanishevsky's pyranometer) was used for daily continuous registration of the total solar radiation incident to the sea surface (PAR_s). The amount of PAR_s during the daytime was taken equal to 50% of the total solar radiation incident to the surface of the sea (Tooming and Gulyaev 1967) and corrected for reflection by the water surface: 3% in the midday, 20% during the first and the last hours of the light day and 10% at the second and penultimate hours of the day. Moreover, from the attenuation of the PAR by the water column in coral habitats and from the PAR_s values during a day, we calculated the underwater PAR at a given depth at any time of the day both in absolute values of photon flux density, $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and in PAR_s percentage (Jerlov 1976). PAR measurements in algal growth were done with the same underwater photometer, mainly at 1000-1200 local time.

Determinations of pigment contents.

The plant material was ground in a porcelain mortar with glass sand and 90% acetone. Algal and seagrass chlorophylls were extracted with acetone. Chlorophyll content in acetone extracts was measured on a Shimadzu MPS-5000 spectrophotometer. The a and b chlorophyll contents in extracts were assessed using the Vernon formula (Vernon 1960), chlorophyll c_2 , by the formula of Jeffrey and Humphrey (1975), chlorophyll a in red algae was determined by Lie's method (Lie 1978). Phycoerythrin was extracted from red algae with seawater (Lie 1978) and its concentration in the solution was determined as described in O'Carra (1965).

Radiocarbon determination of dependence of photosynthesis on light (P_s vs. I curves)

The radiocarbon method was used to measure the rate of net photosynthesis of macrophytes at different light intensities (Kolmakov and Tarankova 1978). The experiments were run in a thermostated chamber, 440 ml in volume, equipped with light filters of different light transmission. Water temperature in the chamber was maintained at 27-28°C. The algae were placed in a chamber filled with seawater onto special grids after which the chamber was closed with a set of neutral light filters and heat filter (0.2% solution of CuSO_4). A high-pressure luminescent lamp was used as the source of light. Under various light filters, in the chamber cells, PAR was equal to 8, 15, 60, 160, 250, 380 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

At the beginning of the experiment the plants were kept in running seawater for 20 min under the light filters. This period was sufficient to obtain a stabilization of physiological processes in the plants transferred into experimental conditions (Titlyanov 1978). The water was then substituted for radioactive carbonate dissolved in seawater (2.5 mM, the initial concentration of HCO_3^- in seawater was 2.0-2.3 mM), specific radioactivity of 100 MBk·ml⁻¹. After a 20 min exposure to light and continuous stirring of water in the chamber on a laboratory shaker, the samples were taken out, washed thoroughly with seawater for 15 min, fixed at 105°C, and dried to constant weight at 60-70°C. The material was not treated with acid to remove radioactive inorganic carbon, assuming that the amount left in the thalli was about equal to the amount of non-radioactive carbon assimilated during the first minutes of exposure. The samples were dried to a constant weight, weighed, ground on a micro-mill and stuffed into cells. The final preparation was a cylindrical tablet 2 mm thick and 0.5 cm² in area. The radioactivity in these tablets (in a layer of full radioabsorption) was determined by the end-type counter T-25-BFL on a recounting instrument with 5% measuring efficiency. The rate of net photosynthesis was calculated in mg CO_2 ·g dry wt⁻¹·h⁻¹ by the following formula:

$$P = \frac{N_r}{K_r \cdot a_c \cdot t}, \text{ where}$$

N_r , was the radioactivity of the material, emissions·min⁻¹;

a_c , the specific radioactivity of the introduced carbonic acid MBk·mg CO_2 ⁻¹;

t , the exposure time, h;

K_r , coefficient, accounting for the physical properties of the tablet of material and for the specific features of the counter (Bykov and Koshkin 1969).

The coefficient K_r was determined experimentally. For this purpose, we took a weighed amount of algae (in g) with a certain amount of radioactive carbon (A, MBk). In tablets with the layer of full radioabsorption the obtained radioactive material was counted in emissions·min⁻¹. Then, according

to the formula,

$$K_r = \frac{N_r m}{A}$$

the coefficient rate was found for the specific plant material, calculated on the recounting instrument. In our experiments, depending on the properties of the material, the K_r coefficient varied from 43.1 to 51.0 emissions·g⁻¹·min⁻¹·MBk⁻¹. The experiments were conducted in triplicate, with double determinations of sample radioactivity.

Analysis of photosynthetic products

The plant samples were placed into an exposure chamber filled with filtered seawater containing radioactive bicarbonate with the specific radioactivity of 550 MBk/mmol H¹⁴CO₃⁻. The algae were exposed with H¹⁴CO₃⁻ to PAR of 300 μE·m⁻²·s⁻¹ for 15, 60 or 300 s. After exposure, the samples were immediately fixed with boiling 80% ethanol and acidified with 5% formic acid. The samples were ground and subjected to full extraction of the alcohol-water-soluble organic fraction, where the extent of radioactivity was determined as emissions·min⁻¹ on a standard counting device (see above). The photosynthetic rate was calculated by the formula:

$$P = \frac{n_1 \cdot V/v + n_2 \cdot M/m}{a_c \cdot t \cdot W \cdot S}, \text{ where}$$

P is the rate of photosynthesis, μmol CO₂·g dry wt⁻¹·h⁻¹;

n_1 , radioactivity of the volume (v , cm³) of a sample of the alcohol-water-soluble fraction, emissions·s⁻¹;

V, the total volume of alcohol-water-soluble fraction, cm³;

M, the total weight of insoluble residual, g;

S, counting efficiency of the radiometric instrument, imp·s⁻¹·MBk⁻¹;

a_c , the specific radioactivity, MBk·mmol CO₂⁻¹;

t, the time of exposure, h;

W, the weight of tested material, g dry wt;

n_2 , radioactivity of the weight (g) of a sample of insoluble residual in emissions·s⁻¹.

The composition of metabolic products was determined by two-dimensional ascending chromatography in the solvent systems described earlier (Bil' et al. 1981). The amount of individual radioactive products, determined chromatographically, was expressed in % of the total.

Adaptation of algae to light and dissolved inorganic nutrients

Seaweeds sampled from the reef-flat intertidal zone, i.e. *Thalassodendron ciliatum* and its epiphytes *Ulva rigida* and *Geldiopsis* sp., were placed in an aquarium with about 30-20% PAR_s and in two aquaria with artificial illumination having PAR of 240 and 90 μE·m⁻²·s⁻¹, respectively. The plants were evenly illuminated and did not shade each other in the aquaria; the water temperature was maintained at 28°C with a photoperiod of 12 hours. After acclimation of the plants for 10 days, the chlorophyll and phycoerythrin contents were determined for one group of plants and light dependence of photosynthesis was analyzed. Another group of plants was fertilized with dissolved inorganic nutrients for two hours under the above light conditions. The final concentrations of salts were 10 mM for NH₄Cl and 1 mM for KH₂PO₄. Then the plants were placed back in the aquaria and kept there for another three days in the same light regimen before analysis of the pigment

content and determination of the rate of photosynthesis.

RESULTS

Pigment content of macrophytes in relation to depth and light

Table 2 shows the results of analyses for pigment content in algal thalli and leaves of seagrasses of the Seychelles Islands sampled from depths from 0 to 50 m on non-shaded sites. In plant associations at shallow depths, it is difficult to find a single plant that is not self-shaded or shaded by other plants in thick growths. Since precise determinations of light absorption by algal associations present technical difficulties, light was measured only approximately (Tables 1, 2, 3). As depth increased from 0 to 37 m, the chlorophyll contents of mature leaves of the seagrass *Thalassodendron ciliatum* increased by 20-30% (Table 2). At a depth of 2-3 m, the chlorophyll content of *Thalassia hemprichii* is 15-20% higher than in material from the intertidal zone. At a depth of 10 m, the content of chlorophyll a in the green alga *Caulerpa cupressoides* showed a 30% increase over intertidal levels. At its maximal depth, about 50 m, *Caulerpa* sp. showed a 50%-decrease in the chlorophyll content compared with material from 25 m.

Table 2 also compares the pigment contents in groups of algae growing at different depths and united by their taxonomic affinity and "life form" (Littler et al. 1983). Laminar and filamentous forms of green algae from the intertidal zone had 50% more pigments than material from depths of 2-4 m, but at 25-30 m, the pigment content was 3.7 times higher than in intertidal forms. Red algae with filamentous branched thalli are also capable of concentrating chlorophyll and phycoerythrin in deep waters; e.g., *Wrangelia argus* from 30 m contained 3.5 times more chlorophyll a and 1.8 times more phycoerythrin than five other shallow-water species of Rhodophyta. It is interesting to examine the distribution of pigments within thalli of *Sargassum cristaefolium* sampled from algal thickets. Here, as a result of intraspecific-shading, the illumination of phyllodes decreased from the top to the base from 100% to 5% PAR_s, whereas the pigment content in phyllodes increased 2.5 times. With shading, the chlorophyll concentration increased also in the pneumatocysts of *Sargassum* plants. Calculating the average content of the sum total of chlorophylls a and b in seagrasses in mg·g wet wt⁻¹, we obtain the following depth-dependent distribution: 1.4±0.8 for 0 m, 1.6±1.2 for 0.5-2 m, 1.7±1.0 for 10-25 m, and 1.8±1.2 mg·g dry wt⁻¹ for 30-50 m. Thus, from 0 to 30-50 m deep, all algal and seagrass species showed a mean 36% increase in chlorophyll content.

Light dependence of photosynthesis during light hours

Variations in the dependence of net photosynthesis on light (P_s vs. I curve) during the day were studied in 13 species at 0700-0900, 1000-1300, and 1600-1800 local time. To compare patterns of photosynthetic dependence on light for all of the species examined, the rates were recalculated in relative units; i.e., 100% corresponded to the maximal rate of photosynthesis obtained during the day in plants of each species investigated at a particular depth. All plants were divided into three groups: those from shallow depths of 0-2 m, from medium depths of 10-15 m and from maximal depths of 25-50 m. For each plant group, the average light curves of photosynthesis were plotted in relative units for the morning, midday and evening (Fig. 1). A majority of the plants showed changes in P_s vs. I curves during the day. From morning to midday hours, photosynthetic light saturation values (I_k) and the initial slope α of each P_s vs. I curve or the efficiency of the use of weak light increased. The first half of the day showed a considerable increase (50-70%) in photosynthetic capacity. During the evening hours, the opposite patterns were observed: the level of photosynthesis on the light curve plateau decreased again to the morning rates, or lower in most cases, and the angle of the initial slope of P_s vs. I curve also diminished. Plants inhabiting different depths have different kinds of

daily changes of their P_s vs. I curves. For example, in the evening hours, a photon flux density of $250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ inhibits the photosynthesis of deep-water plants, and at $380 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, the rate of photosynthesis is nearly half of the maximal rate at these hours. In plants from the intertidal zone, the initial linear slope of the light curve (α) decreases less than in deep-water plants.

The variations described above in light-dependence of photosynthesis were also observed in the phyllodes of *Sargassum cristaefolium*, taken from differently illuminated parts of the plant (Fig. 2). Here, as with depth dependence, a decrease in phyllodes illumination entails the loss of photosynthetic resistance to increased light intensity in the evening. In the shaded parts of plants, the change in the slope of α is greater during the day.

Fig. 3 depicts changing photosynthetic efficiencies in the use of incident light of different intensities during the day for deep-water samples of the seagrass *Thalassodendron ciliatum* and two green algae. All plants exhibited the same patterns. The photosynthetic efficiency of the use of weak light ($15 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) increased from 0700 to 1100-1300 by 60-70%. Following 1100 to 1300, the efficiency of weak light use was at its greatest. The midday light of $15 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ was sufficient for deep-water plants to reach 70-80% of their maximum photosynthetic rates. After 1700, the efficiency of the use of weak light dropped to that equivalent to 0700-0800. The efficiency of using light bright enough to achieve photosynthetic saturation ($150 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) increased gradually to 1300 and then decreased considerably towards the evening, however always remaining higher than the morning rates. Inhibition of photosynthesis in deep-water plants by high levels of photon flux density ($\text{PAR} > 380 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) may begin as early as 1300, by evening (1700) photo-inhibition was significant in *Halimeda gracilis* and especially in *Caulerpa* sp.

Capacity of photosynthesis in tropical marine plants at different depths

Measurement of the light dependence of photosynthesis during the day showed that tropical marine plants reach their highest capacities at midday (1200-1300). Plants of the intertidal zone did not differ significantly in the levels of maximum primary production, whereas subtidal plants exhibited considerable differences in the maximum rate of photosynthesis (Fig. 4). The highest photosynthetic capacities were observed in marine plants down to depths of 20-25 m, i.e., to 10% PAR_s . The highest production rates were $17.9 \text{ mg CO}_2\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$ for *Valonia fastigiata* at a depth of 25 m; $12.0 \text{ mg CO}_2\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$ for the upper thallus of *Sargassum cristaefolium*; $9.3 \text{ mg CO}_2\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$ for *Laurencia corymbosa* at a depth of 10 m and $9.1 \text{ mg CO}_2\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$ for *Thalassodendron ciliatum* at a depth of 23 m. The lowest productive capabilities, i.e., 2.0 to 3.0 $\text{mg C}\cdot\text{g dry wt}^{-1}\cdot\text{h}^{-1}$, were found in *Codium tomentosum*, *Caulerpa brachypus*, *Halimeda opunta* and *Hypnea spinella*.

Variations in photosynthetic light curves P_s vs. I and productive capabilities as a function of depth

Four species of marine plants were compared growing at depths between 0 and 50 m (Fig. 5). Considerable differences in the form of the P_s vs. I curve and productive capabilities of photosynthesis were found in mature leaves of the seagrass *Thalassodendron ciliatum*. The photosynthetic capacity increased with depth up to 25-30 m, but decreased at the maximum depth (33-37 m) and accounted only for 30% that of shallow sites. With increasing depth, the initial slope of the P_s vs. I curve (α) more than doubled when PAR diminished from 90 to 10% PAR_s and was lower at greater depths. In specimens of *T. ciliatum* inhabiting the greatest depths, photosynthetic inhibition by light exceeding $250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. *Laurencia corymbosa* also showed higher photosynthetic capacity and a steeper initial slope of the P_s vs. I curve when PAR decreased from 90 to 30% PAR_s with depth. A similar depth-dependent decrease in PAR caused negligible but

opposite changes in the light dependence of photosynthesis in the green alga *Caulerpa cupressoides*. In habitats with less than 5% PAR_s , *Caulerpa* sp., growing abundantly at depths of 40-50 m near Astove island, loses its net photosynthetic abilities.

Acclimation of tropical marine plants to PAR under experimental conditions

Three plant species were used in this experiment, the seagrass *Thalassodendron ciliatum*, occurring on the reef flat in the intertidal zone and two of its epiphytes, *Ulva rigida* and *Gelidiopsis* sp. We tested the effect of lowered light intensities on the photosynthetic pigment content and photosynthesis in the above species (Table 3). Compared with the initial levels, the content of chlorophylls and phycoerythrin increased in plants during a 10-day experiment with considerably lowered PAR, $90 \mu E \cdot m^{-2} \cdot s^{-1}$. After fertilization with dissolved inorganic nutrients (3 h) and subsequent retention of the plants for three days under the same lowered intensity in water without nutrients, the chlorophyll content in *U. rigida* increased again by 30%, but only when the photon flux density was $90 \mu E \cdot m^{-2} \cdot s^{-1}$. Only under these experimental conditions did *Gelidiopsis* sp. show considerably elevated chlorophyll a and phycoerythrin contents. The chlorophyll content in leaves of *T. ciliatum* changed insignificantly and without apparent pattern in all conditions of the nutrient-enrichment experiment.

The dependence of net photosynthesis on light also was analyzed (Fig. 6). Although the results are not presented in this article, we did not detect any significant differences in the character of the P_s vs. I curves under different conditions of the experiment in the seagrass *Thalassodendron ciliatum*. The decrease in light intensity to $90 \mu E \cdot m^{-2} \cdot s^{-1}$ reduced the photosynthetic capacity of *Ulva rigida* by 50% compared to that at $240 \mu E \cdot m^{-2} \cdot s^{-1}$ and also more than doubled the angle of initial slope of the photosynthetic light curve α . When fertilized with N and P, *U. rigida* did not change its photosynthetic capacity but α increased.

In the red alga *Gelidiopsis* sp., at $90 \mu E \cdot m^{-2} \cdot s^{-1}$, the light curve of photosynthesis had a steeper initial slope than at $240 \mu E \cdot m^{-2} \cdot s^{-1}$, but showed a lower photosynthetic light saturation value. Fertilization increased the photosynthetic capacity and α of *Gelidiopsis* sp. under both light conditions, especially when the photosynthetic light saturation value was 2.4 times as high as in algae without nutrients.

The path of carbon in photosynthesis

Table 4 gives the composition of primary products of photosynthesis in two species of seagrasses and six seaweeds occurring in stressful conditions of intertidal pools and in the upper subtidal at shallow depths. Our analysis revealed that in all species of marine plants studied, 3-phosphoglyceric acid was the first stable product of photosynthesis, accounting for 100-50% of all labeled primary photosynthetic products in plants after 15 s of exposure to light with $H^{14}CO_3^-$. With longer exposures, e.g. 300 s, labeled carbon transforms uniformly from 3-phosphoglyceric acid into non-phosphoralated sugars. Environmental conditions do not change the distribution and redistribution patterns of the label in the intermediate and definitive products of photosynthesis. Only in one case, in the seagrass *Thalassia hemprichii* growing in the intertidal zone, 28% of the radioactive carbon of primary products was found in asparaginic acid during the first 15 s of exposure. However, the character of redistribution of the label does not permit a conclusion on the primary synthesis of aspartate.

DISCUSSION

Adaptation of tropical seaweeds and seagrasses to different light intensities

It was shown earlier that most species of temperate macroalgae have the *Ulva*-type of adaptation, that is, a considerable variety of responses enabling them to acclimate to a wide range of light intensities; for most species from 100-80% to 5-3% PAR_s and for some, up to 0.1 or even 0.05% PAR_s (Titlyanov 1983, Titlyanov et al. 1987). The following are, in our view, most common responses of the *Ulva*-type marine plants to reduced light intensities: 1) accumulation of photosynthetic pigments in chloroplasts and increasing the size of photosynthetic units (Lie and Titlyanov 1978, Leletkin 1981); 2) increasing the efficiency of the use of absorbed light (Titlyanov et al. 1987); 3) increasing the content of photosynthetic units per weight of tissue and the area of thallus surface (Leletkin 1981, Titlyanov et al. 1987); 4) increasing the size of chloroplasts and the number of photosynthetic membranes in chloroplasts (Titlyanov et al. 1974); 5) increasing photosynthetic capacity (Titlyanov et al. 1987).

How do tropical marine plants adapt themselves to light? Scarce data (O'Neal and Prince 1982, Titlyanov et al. 1983, Littler et al. 1988) and general theoretical speculations (Littler and Littler 1988) lead us to believe that tropical and temperate species of seaweeds and seagrasses have similar mechanisms and reactions of adaptation to light. However, tropical macrophytes are subjected to environmental effects that differ considerably from those in temperate zones. Examples are extremely high temperatures in the intertidal zone, a weak temperature stratification of the water column and a low content of dissolved inorganic nutrients. Species composition of tropical waters differs greatly from that of the temperate zone. Calcareous green and red algae are dominant and vast expanses are covered by seagrasses (Littler and Littler 1988). Crustose and massive forms are numerous among the growth forms and epiphytism is widespread (Littler and Littler 1988).

Our investigations on 27 species of seaweeds and seagrasses have shown that the basic adaptive reactions mentioned above do manifest themselves in the tropics. Still, in spite of a wide range of changing light intensities, the range of variations of the physiological characters of photosynthesis is much narrower than in plants of the temperate zone. For example, the photosynthetic pigment content in plants of the temperate zone may change 6-7 fold, depending on habitat illumination (Lie and Titlyanov 1978), whereas in the tropics we recorded only 3.5-fold changes. There is a general low level of chlorophyll content and especially phycoerythrin in marine tropical plants. The highest content of these pigments occurred in deep-water species: chlorophyll *a* in *Avrainvillea amadelpha* = 0.52 mg·g wet wt⁻¹ and phycoerythrin in *Wrangelia argus* = 0.89 mg·g wet wt⁻¹. In the temperate zone, contents such as 1.2-0.8 mg·g wet wt⁻¹ for chlorophyll *a* and 4-2 mg·g wet wt⁻¹ for phycoerythrin are not rare (Lie and Titlyanov 1978). What are the causes of these differences? Perhaps they are reflective of a shortage of dissolved inorganic nutrients, especially nitrogen, in tropical waters. Our experiments on algal adaptation to low light intensity against the background of fertilization with inorganic nutrients support this speculation. Tropical algal species also have less capability to increase the efficient use of weak light. Lower photosynthetic light saturation is one mechanism of adaptation of tropical algae and especially seagrasses to the use of solar radiation over a wide range. In most species investigated, irrespective of the place of growth, photosynthesis was saturated even at 40-90 $\mu E \cdot m^{-2} \cdot s^{-1}$. Such a low light saturation level is also typical of algae of temperate latitudes, but particularly those growing under extreme low light conditions (Titlyanov et al. 1987).

The seagrass *Thalassodendron ciliatum* is a special case which, like a majority of algal species investigated, exhibits the above adaptive reactions but to a far lesser extent than macroalgae. Adaptation of *T. ciliatum* to a wide range of illumination intensities, from 100 to 8% PAR_s , is mainly due to an extremely low light saturation, a high content of chlorophylls, 1-2 mg·g wet wt⁻¹ and a great photosynthetic capacity at saturating light intensities (7-9 mg CO₂·g dry wt⁻¹·h⁻¹).

Diurnal changes in light dependence of algal photosynthesis

It was shown earlier that light dependence of algal photosynthesis is variable throughout the day (Titlyanov et al. 1978), but until recently little attention has been given both to the study of mechanisms responsible for daily photosynthetic changes and to calculations of primary production. All species of marine plants investigated here showed variations in the pattern of photosynthetic light curves during the day. These changes were as follows: the photosynthetic capacity rose from the morning to midday hours and decreased towards the evening. These changes were considerable and the potential photosynthetic activity of algae at midday was 1.5-2 times higher than in the morning, which is comparable to similar algal reactions in temperate latitudes (Titlyanov et al. 1978). Along with the increased photosynthetic capacity, the efficiency of the use of weak light also increased toward midday; i.e., the initial slope of the P_s vs. I curve steepened. This pattern reversed during the second half of the day. Photosynthesis is inhibited by a photon flux density above $250 \mu E \cdot m^{-2} \cdot s^{-1}$. PAR in excess of $380 \mu E \cdot m^{-2} \cdot s^{-1}$ reduces the photosynthetic rate of deep-water algae as early as 1300. These PAR intensities never inhibited photosynthesis in algae and seagrasses during the morning. The observed daily changes in the functioning of the photosynthetic apparatus of algae and seagrasses needs further elucidation.

Productive capacities of tropical marine plants

This study shows that tropical algae and seagrasses maintain a constant level of productive capabilities within a rather wide range of illumination intensities, i.e. from 100 to 15% PAR_s , and only deep-water species, which receive no more than 10-8% PAR_s , reduce their photosynthetic capacity 2.5-3 fold. Stressful conditions of the intertidal zone do not significantly lower photosynthesis of algae and seagrasses. Maximal rates of net photosynthesis ranged from 18 to 2 $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ in different algal and seagrass species. The highest rate of photosynthesis was in *Sargassum* (10-12) $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$, green laminar algae (7-18); red algae with filamentous highly branched thalli (7-9) and seagrasses (7-10). The lowest capacity of net photosynthesis was in algae of the genus *Halimeda* (2-3) $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$. Our data on the maximum net production of algae and seagrasses obtained with the use of the radiocarbon method approximate those obtained in the expedition by I. I. Cherbadji who used the oxygen technique. According to his unpublished data, the maximum daily net photosynthesis, evaluated as $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$, was for *Enteromorpha* sp.: 20; *Thalassodendron ciliatum* (whole plant with the stalk and roots): 3-4; *Sargassum* sp. (whole plant): 6; *Padina* sp.: 8; *Caulerpa cupressoides*: 4; *Halimeda* sp. (whole plant): 0.7 $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$. Other data show that the net photosynthesis of the genus *Halimeda* from deep waters of the Bahamas fluctuated from 1.3 to 4.8 $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ (Jensen et al. 1985). The net photosynthesis of *Caulerpa paspaloides* in Florida fluctuates, depending on season, from 0.8 to 6 $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ (O'Neal and Prince 1982). The highest rates of net photosynthesis in algae of the Belize Barrier Reef were as follows: *Acanthophora spicifera*, 15; *Dictyota divaricata*, 21; *Halimeda opuntia*, 7 $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ (Lapointe et al. 1987). According to many authors, different species of *Halimeda* have rates of net photosynthesis varying from 2.1 to 6.7 $mg CO_2 \cdot g \text{ dry wt}^{-1} \cdot h^{-1}$ (Littler et al. 1988). Thus, the data on the maximum net production of macrophytes in the Seychelles Islands are similar to those obtained from other tropical regions of the world.

The path of carbon in photosynthesis of macrophytes

The data we obtained on the path of carbon in photosynthesis of tropical species of algae and seagrasses provide additional support of the earlier idea (Titlyanov 1983) that there are no species among marine multicellular algae with photosynthesis on the C_4 - path. In certain situations; e.g., in very low light (Yadykin and Titlyanov 1980), during the sporogenetic stage (Kolmakov et al. 1985),

large amounts of amino-acids such as aspartate and alanine emerge in the early products of photosynthesis to suggest the outflow of 3-phosphoglyceric acid from the Calvin cycle into alternative paths and active β -carboxylation. Such changes in the orientation of photosynthetic carbon metabolism have been noted in the tropical seagrasses *Thalassia hemprichii*.

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Table 1. Marine plants and their habitats.

Plant species Growth form	Habitat, conditions	Depth, m	Illumination, % PAR _s
Angiospermae			
1. <i>Thalassodendron ciliatum</i> (Forskål) den Hartog	Islands of Cœtivy, Farquhar, Aldabra, intertidal pools	0	80-100
	Farquhar, Desroches, upper subtidal	0.5	50-90
	Cœtivy, Farquhar, Providence, upper, subtidal, high sedimentation, dense growth	2	40-70
	Cœtivy, dense growth	11	30-50
	Desroches, dense growth	13	30-50
	Aldabra, single patches on sand	15	10-20
	African Banks, on coral debris, dense growth	17	10-15
	Providence, dense growth on coral debris	20	10-15
	Cœtivy, growth on coral debris	23	12-16
	African Banks, dense growth	25	5-10
	Cœtivy, Providence, from sparse growths to single plants	33	8-10
	African Banks, sparse growths	37	8-10
2. <i>Thalassia hemprichii</i> (Ehrenb.) Aschers	Farquhar, intertidal pools	0	100

Table 1. Continued.

Chlorophyta			
3. <i>Avrainvillea amadelpha</i> Gepp, large leathery lamellae	Saint Joseph, single plants on coral pebble	30	10-12
4. <i>Boodlea struveoides</i> Howe filamentous, assembled in "pads"	Aldabra, intertidal pools single "pad" assemblages	0	100
5. <i>Caulerpa cupressoides</i> (West) Ag. massive filaments	Cosmoledo, intertidal drained pools, single plants	0	100
	upper subtidal, among corals, partly covered by sand	7-10	50-60
6. <i>Caulerpa brachypus</i> leathery laminated phyllodes	Cosmoledo, intertidal drained pools	0	50-60
	Astove, upper subtidal opposite to the passage to lagoon	0.5	60-90
7. <i>Caulerpa</i> sp. thick watery phyllodes	Aldabra, upper subtidal single plants	25	10-13
8. <i>Codium tomentosum</i> (Huds.) Stackh. thick branched thallus	Saint-Joseph, upper subtidal, single plants on coral debris	30	10-12
9. <i>Dictyosphaeria cavernosa</i> (Forskål) Boerg laminated thallus	Farquhar, deep intertidal pools, single plants	0.5	80-90
10. <i>Enteromorpha kyllinii</i> Bliding thin, filamentous	Aldabra, intertidal pool, epiphytes on <i>Thalassodendron ciliatum</i>	0	60-100
11. <i>Enteromorpha</i> sp. filamentous, thin	Providence, upper subtidal and intertidal, among sand on coral fragments	0-0.5	90-100

Table 1. Continued.

12. <i>Halimeda gracilis</i> Harv. et Ag. calcareous, thin	Aldabra, upper subtidal,	25	10-13
13. <i>Halimeda micronesica</i>	Aldabra, intertidal pools, dense pads among other algae	0	60-100
14. <i>Halimeda opuntia</i> (Linn.) Lam calcareous, thick	Saint Joseph, upper subtidal single plants	30	10-12
15. <i>Halimeda tuna</i> (Ell. and Sol) Lam calcareous, thick	Saint Joseph, upper subtidal single plants	30	10-12
16. <i>Udotea orientalis</i> A et E Gepp laminated thalli	Saint Joseph, upper subtidal tidal, single plants	30	10-12
17. <i>Ulva rigida</i> C. Ag. laminated thallus	Aldabra, deep intertidal pools, strong current, epiphytes of <i>Thalassodendron ciliatum</i> stalks	0.5	60-90
18. <i>Valonia aegagropila</i> (Roth) Ag. thick watery crust	Aldabra, upper subtidal, single plants	25	10-13
Phaeophyta			
19. <i>Dictyopteris delicatula</i> Lam. laminated, thin	Saint Joseph, upper subtidal, single plants on coral debris	30	10-12
20. <i>Sargassum cristaefolium</i> C. Ag. laminated leathery phylloids	Praslin, upper subtidal, dense growths, heavy self-shading	30	10-12
21. <i>Turbinaria ornata</i> (Turn) J. Ag. massive thalli	Aldabra, intertidal pools, single plants	0	80-100
Rhodophyta			
22. <i>Acanthophora spicifera</i> (Vahl) Boer thin branched	Astove, lagoon, intertidal and upper subtidal growths over the <i>Thalassia hemprichii</i>	0-0.5	50-100

Table 1. Continued.

23. <i>Gelidiopsis</i> sp. thin branched	Aldabra, upper subtidal, strong current, epiphytic on <i>Thalassodendron</i> <i>ciliatum</i> stalks	0.5	60-90
24. <i>Hypnea spinella</i> (C. Ag.) Kütz. filamentous, branched	Cosmoledo, intertidal pools sometimes drained	0	100
25. <i>Laurencea corymbosa</i> J. Ag., thin branched	Cosmoledo, intertidal pools	0	100
26. <i>Laurencia</i> sp. thin, branched	Aldabra, intertidal pools, sometimes drained		
27. <i>Wrangelia argus</i> (Mont.) Mont. thin, filamentous	Saint Joseph, upper subtidal, single thalli	30	10-12

Table 2. Content of photosynthetic pigments in marine plants. Chl.a = chlorophyll a; Chl.b = chlorophyll b (Green algae); Chl.c₂ = chlorophyll c₂(Brown algae); P = Phycoerythrin (Red algae); * = mean arithmetic values from 3-5 experiments; \pm = standard deviation; ** = mean arithmetical value of two parallel measurements.

Species	Habitat, (m), depth % PAR _s	Chl. a mg·g wet wt ⁻¹	Chl. b mg·g dry wt ⁻¹	Chl. c ₂ mg·g wet wt ⁻¹	P mg·g dry wt ⁻¹
In samples of one species from different depths					
<i>Thalassodendron ciliatum</i> (seagrass)					
	Cœtivy, Farquhar, Aldabra, intertidal zone, 0, 100	0.72 \pm 0.06	2.4 \pm 0.2	0.43 \pm 0.1	1.4 \pm 0.3
	Cœtivy, Farquhar, Providence, 2, 80	0.63 \pm 0.06	1.98 \pm 0.3	0.32 \pm 0.1	1.08 \pm .3
	Cœtivy, Desroches, Aldabra, African Banks, 11-17;40-20	0.81 \pm 0.1	2.75 \pm 0.2	0.45 \pm 0.1	1.54 \pm 0.4
	Cœtivy, Providence, African Banks, 33-37; 10-8	0.89 \pm 0.2	2.8 \pm 0.6	0.49 \pm 0.2	1.68 \pm 0.8
<i>Thalassia hemprichii</i> (seagrass)					
	Farquhar intertidal zone, 0,100	0.57**	1.7	0.27	0.81
	Farquhar, 2,60	0.67	2.0	0.27	0.81
<i>Caulerpa cupressoides</i> (green alga with massive thallus)					
	Cosmoledo intertidal zone 0,100	0.10	0.6	0.06	0.36
	Cosmoledo, 10,30	0.13	0.78	0.06	0.36
<i>Caulerpa</i> sp. (green alga with massive thallus)					
	Aldabra 25, 10	0.17	1.0	0.09	0.54
	Astove 50, 5	0.11	0.66	0.06	0.36

Table 2. Continued.

Species	Habitat, (m), depth % PAR _s	Chl. a mg·g wet wt ⁻¹	Chl. b mg·g dry wt ⁻¹	Chl. c ₂ mg·g wet wt ⁻¹	P mg·g dry wt ⁻¹
In differently illuminated plant parts					
<i>Sargassus cristaefolium</i>					
Praslin, upper thallus 0, 5, 90					
	phyllodes	0.18	0.4	0.03	0.07
	pneumatocysts	0.12	0.27	0.02	0.04
middle thallus 1,30					
	phyllodes	0.45	0.62	0.05	0.11
	pneumatocysts	0.21	0.46	0.04	0.09
lower thallus 1.5, 5					
	phyllodes	0.45	1.0	0.07	0.15
	pneumatocysts	0.20	0.4	0.04	0.09
In filamentous and laminated green algae					
<i>Boodlea struveoides</i>					
	Aldabra, intertidal zone, 0, 100	0.15	0.97	0.07	0.46
<i>Enteromorpha kylinii</i>					
	Aldabra, intertidal zone, 0, 100	0.19	1.1	0.07	0.40
<i>Ulva rigida</i>					
	Aldabra, intertidal zone, 0, 100	0.15	1.0	0.07	0.48
<i>Dictyosphaeria cavernosa</i>					
	Cosmoledo intertidal zone, 0, 100	0.05	0.39	0.02	0.16
<u>Average of the four species</u>		<u>0.14±0.05</u>	<u>0.86±0.32</u>	<u>0.06±0.02</u>	<u>0.37±0.12</u>

Table 2. Continued.

Species	Habitat, (m), depth % PAR _s	Chl. a mg·g wet wt ⁻¹	Chl. b mg·g dry wt ⁻¹	Chl. c ₂ mg·g wet wt ⁻¹	P mg·g dry wt ⁻¹
<i>Microdictyon montagnei</i> Providence, 2, 80		0.14	0.77	0.08	0.44
<i>Enteromorpha</i> sp. Providence, 2, 80		0.09	0.3	0.05	0.17
<u>Average of the two species</u>		<u>0.11±0.03</u>	<u>0.53±0.23</u>	<u>0.07±0.02</u>	<u>0.3±0.1</u>
<i>Avrainvillea amadelpha</i> St. Joseph, 30, 10		0.58	1.16	0.37	0.74
<i>Udotea orientalis</i> St. Joseph, 30, 10		0.46	0.92	0.19	0.38
<u>Average of the two species</u>		<u>0.52±0.08</u>	<u>1.04±0.12</u>	<u>0.28±0.12</u>	<u>0.56±0.18</u>
<i>Laurencia</i> sp. Aldabra intertidal zone, 0, 100		0.10	0.67	0.67	4.49
<i>Gelidiopsis</i> sp. Aldabra intertidal zone, 0, 100		0.06	0.3	0.86	3.7
<i>Laurencia corymbosa</i> Cosmoledo intertidal zone, 0, 100		0.06	0.4	0.27	1.8
<i>Hypnea spinella</i> Cosmoledo intertidal zone, 0, 100		0.05	0.33	0.22	1.43
<i>Acanthophora spicifera</i> Astove intertidal zone, 0, 100		0.05	0.35	0.36	2.52
<u>Average of the five species</u>		<u>0.06±0.02</u>	<u>0.41±0.07</u>	<u>0.48±0.2</u>	<u>3.0±0.4</u>

Table 2. Continued.

Species	Habitat, (m), depth % PAR _s	Chl. a mg·g wet wt ⁻¹	Chl. b mg·g dry wt ⁻¹	Chl. c ₂ mg·g wet wt ⁻¹	P mg·g dry wt ⁻¹
<i>Wrangelia argus</i> St. Joseph, 30, 10		0.21	1.7	0.89	6.9
Other algae studied					
<i>Halimeda micronesica</i> (green alga, calcified) Aldabra intertidal zone, 0, 100		0.20	0.44	0.21	0.46
<i>Turbinaria ornata</i> (brown alga, massive thallus) Aldabra intertidal zone, 0, 100		0.22	0.53	0.12	0.29
<i>Calulterpa brachypus</i> (green alga, massive thallus) Cosmoledo littoral zone, 0, 100		0.19	1.1	0.09	0.54
<i>Valonea aegagropila</i> (green alga, massive thallus) Cœtivy, 23, 16		0.05	0.43	0.02	0.26
<i>Halimeda gracilis</i> (green alga, calcified) Aldabra 25, 10		0.09	0.54	0.04	0.24
<i>Codium tomentosum</i> (green alga, massive thallus) St. Joseph, 30, 10		0.07	0.32	0.05	0.23
<i>Halimeda tuna</i> (green alga, calcified) St. Joseph, 30, 10		0.13	0.29	0.08	0.18
<i>Dictyopteris delicatula</i> (brown alga, laminated) St. Joseph, 30, 10		0.17	0.77	0.08	0.36

Table 3. Variations in photosynthetic pigment contents of marine plants during the course of adaptation to different light intensities and under fertilization with mineral nitrogen and phosphorus (concentrations: N - 10 mM; N source - NH_4Cl ; P-1mM; source - KH_2PO_4). Pigment values presented with the value for $\text{mg}\cdot\text{g wet wt}^{-1}$ listed above $\text{mg}\cdot\text{g dry wt}^{-1}$.

Species, habitat, depth (m), % PAR_s	Pigments:	Experimental variants					
		Initial variant	Natural light 20% PAR_s	without N and P Artificial light ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$): % PAR_s		with N and P 240:20 90:8	
<i>Ulva rigida</i> Aldabra, inter- tidal zone 0; 60-20	Chl. a	0.15	0.16	0.15	0.21	0.15	0.27
		0.9	0.96	0.6	1.26	0.6	1.62
	Chl. b	0.07	0.09	0.07	0.11	0.07	0.13
		0.42	0.54	0.42	0.66	0.42	0.78
<i>Gelidiopsis</i> sp. Aldabra, inter- tidal zone 0; 60-20	Chl. a	0.06	0.05	0.05	0.07	0.05	0.12
		0.32	0.27	0.27	0.37	0.27	0.64
	P	-	0.49	0.37	0.60	0.41	0.70
		-	2.6	1.96	3.18	2.17	3.7
<i>Thalassodendron</i> <i>ciliatum</i> Aldabra inter- tidal zone; 0; 100-80	Chl. a	0.64	0.61	0.62	0.62	0.40	0.54
		2.18	2.07	2.1	2.1	1.36	1.84
	Chl. b	0.27	0.28	0.29	0.29	0.18	0.28
		0.92	0.95	0.98	0.95	0.61	0.95

Table 4. Composition of primary products of photosynthesis in marine plants collected from intertidal pools and the upper subtidal zone of Aldabra Atoll. * = phosphoric ethers of sugars, PhES; 3-PhGA, 3-phosphoglyceric acid; ** - "Sugars" indicates the sum of saccharose, glucose, fructose etc.

Species	Time of exposure on light with C^{14} , s	Radioactivity of alcohol-water-soluble fraction. % of total							
		3-PhGA + PhES *	** Sugars	Asp- artate	Gluta- mate	Alanine	Serine+ Glycine	Malate	Unidentified
<i>Thalassodendron ciliatum</i>	15	76.3	8.3	6.5	-	1.1	1.1	-	6.1
	60	39.1	37.7	6.1	5.4	3.3	2.5	3.1	2.8
	300	5.1	73.2	4.3	0.7	3.3	9.8	-	3.6
<i>Thalassia hemprichii</i>	15	55.7	4.4	27.9	-	4.2	7.9	-	-
	60	13.6	54.3	17.0	-	2.1	7.9	2.1	3.0
	300	6.7	55.3	7.4	0.3	3.0	23.1	-	4.2
<i>Enteromorpha kylinii</i>	15	93.6	1.1	-	-	1.8	-	-	3.5
	60	87.2	1.9	3.5	1.0	5.0	-	-	1.4
	300	61.5	16.5	5.6	4.2	10.2	-	-	1.8
<i>Ulva rigida</i>	15	94.6	1.7	0.3	-	2.8	0.7	-	-
	60	89.1	2.9	3.1	-	2.8	-	-	2.1
	300	59.1	13.7	7.6	2.2	8.7	2.4	5.1	1.0
<i>Boodlea struveoides</i>	15	83.4	-	1.1	3.2	9.1	0.6	-	6.6
	60	28.5	-	2.8	1.3	11.5	-	-	1.9
	300	33.9	33.2	4.4	9.4	9.3	9.9	-	-
<i>Turbinaria ornata</i>	15	58.7	36.5	3.0	-	1.8	-	-	-
	60	18.8	74.9	3.0	-	3.3	-	-	-
	300	12.8	72.1	5.0	0.8	5.0	2.3	-	2.0
<i>Laurencia</i> sp.	15	100.0	-	-	-	-	-	-	-
	60	85.2	13.1	-	0.9	0.8	-	-	-
	300	52.2	18.2	6.1	1.4	3.7	18.4	-	-
Plants of the upper subtidal zone, depth 0.5 m, 90 - 60 % PAR _s									
<i>Thalassodendron ciliatum</i>	60	50.9	37.2	1.8	2.3	1.4	2.3	2.8	1.3
<i>Ulva rigida</i>	60	93.7	3.0	1.6	-	1.5	-	-	0.2
<i>Gelidiopsis</i> sp.	15	81.4	-	-	-	-	-	-	18.6
	60	86.7	4.2	1.5	-	1.1	6.5	-	-
	300	14.9	62.0	1.6	-	-	21.4	-	-

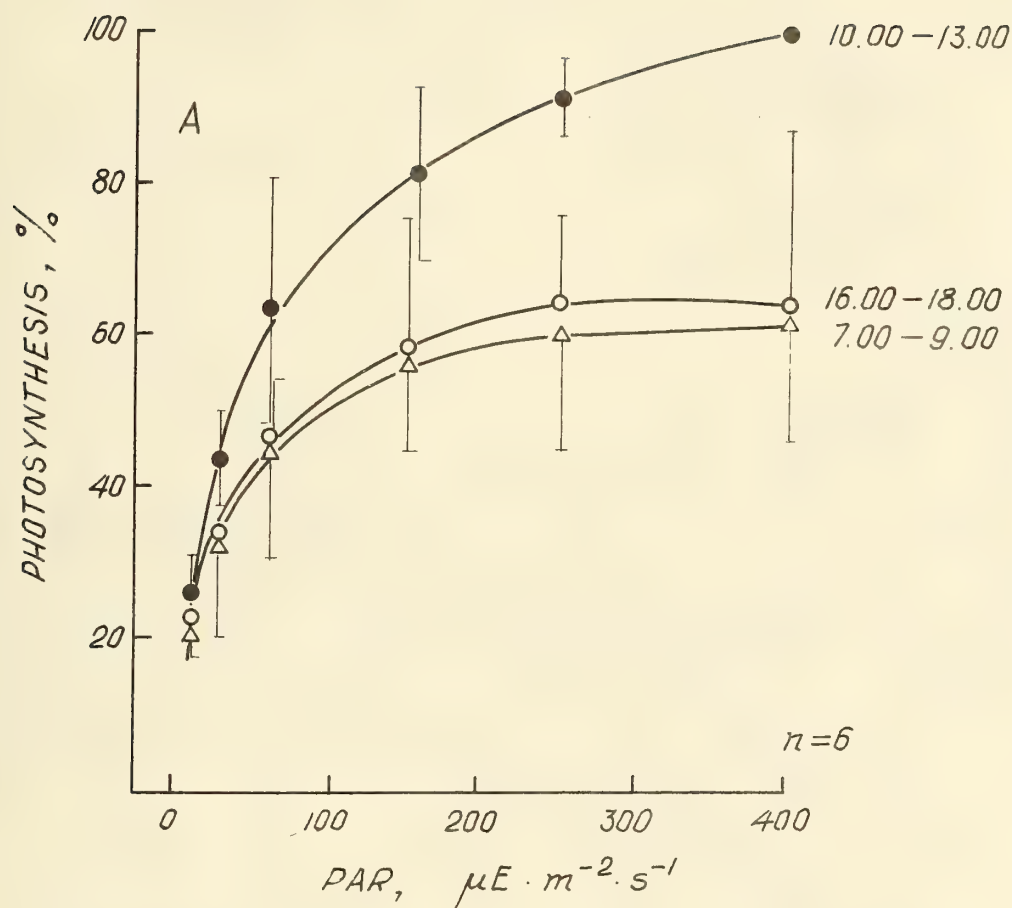


Figure 1 (A). Daily variations in light dependence of marine plant photosynthesis (P_s vs. I curve). A, shallow water plants, 0 - 0.5 m depth, 100 - 90 % PAR_s (*Dictyosphaeria cavernosa*, *Caulerpa cupressoides*, *Hypnea spinella*, *Sargassum cristaefolium*). B, plants of medium depth, 10 - 15 m, 30 - 15 % PAR_s (*Caulerpa* sp., *Codium tomentosum*, *Halimeda tuna*, *Avrainvillea amadelpha*, *Halimeda gracilis*).

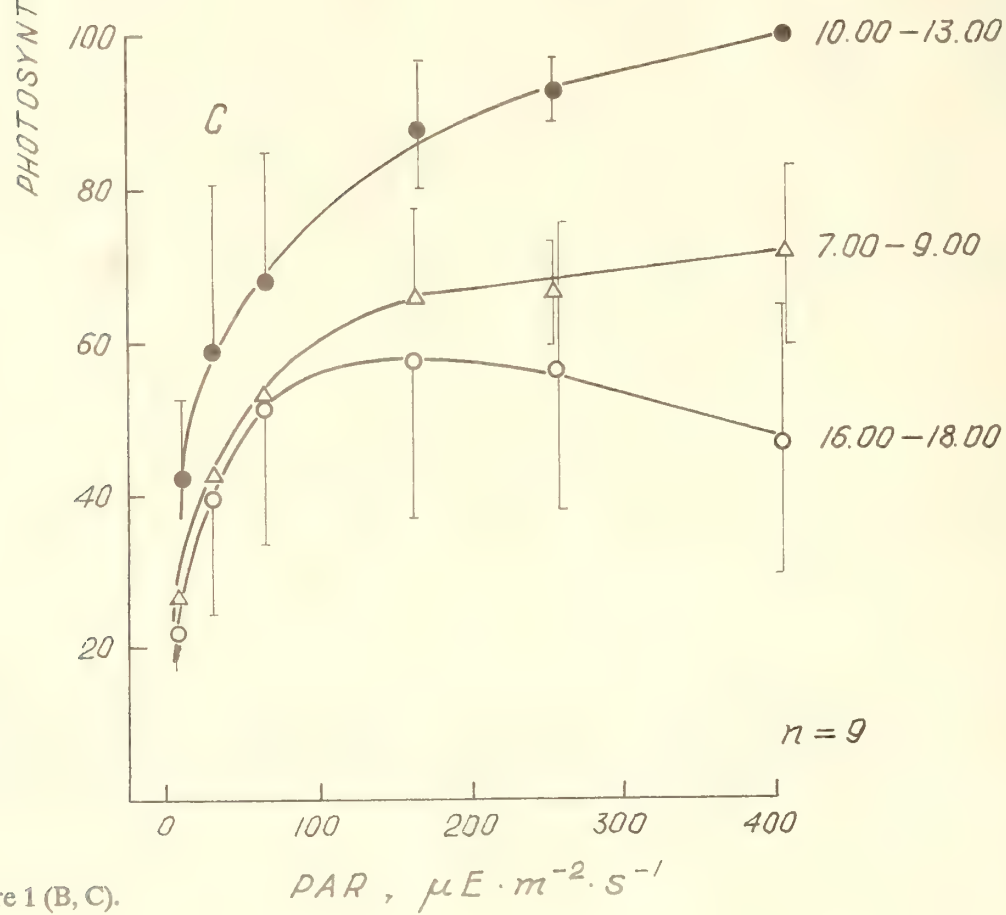
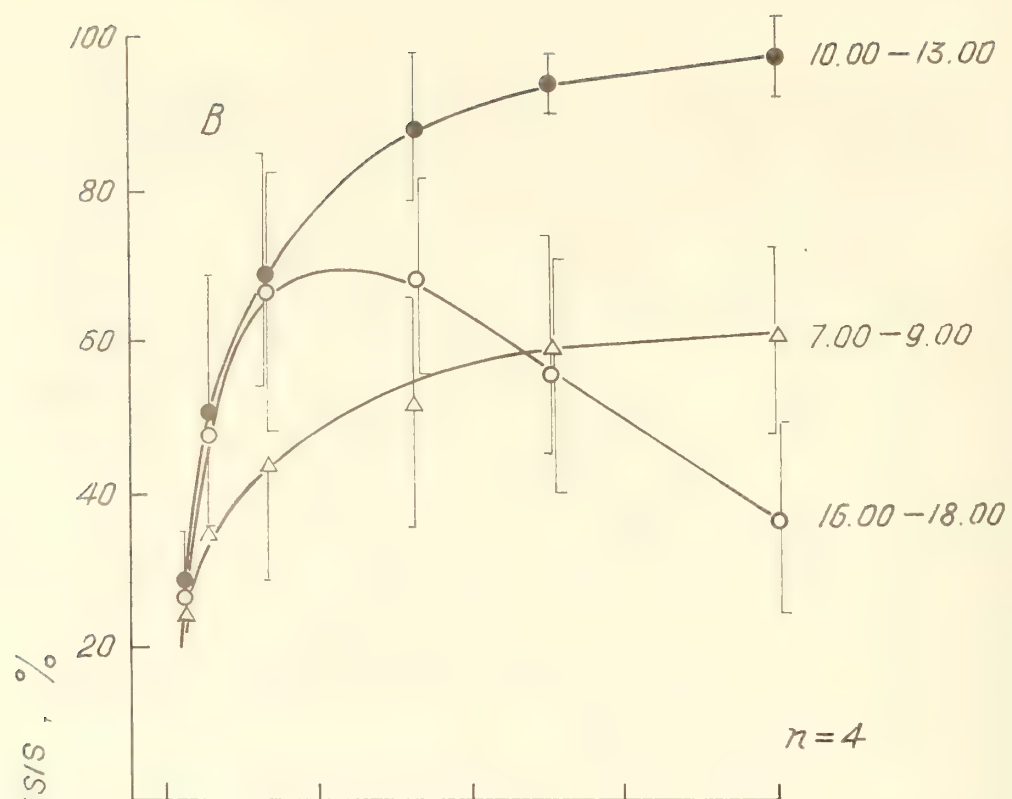


Figure 1 (B, C).

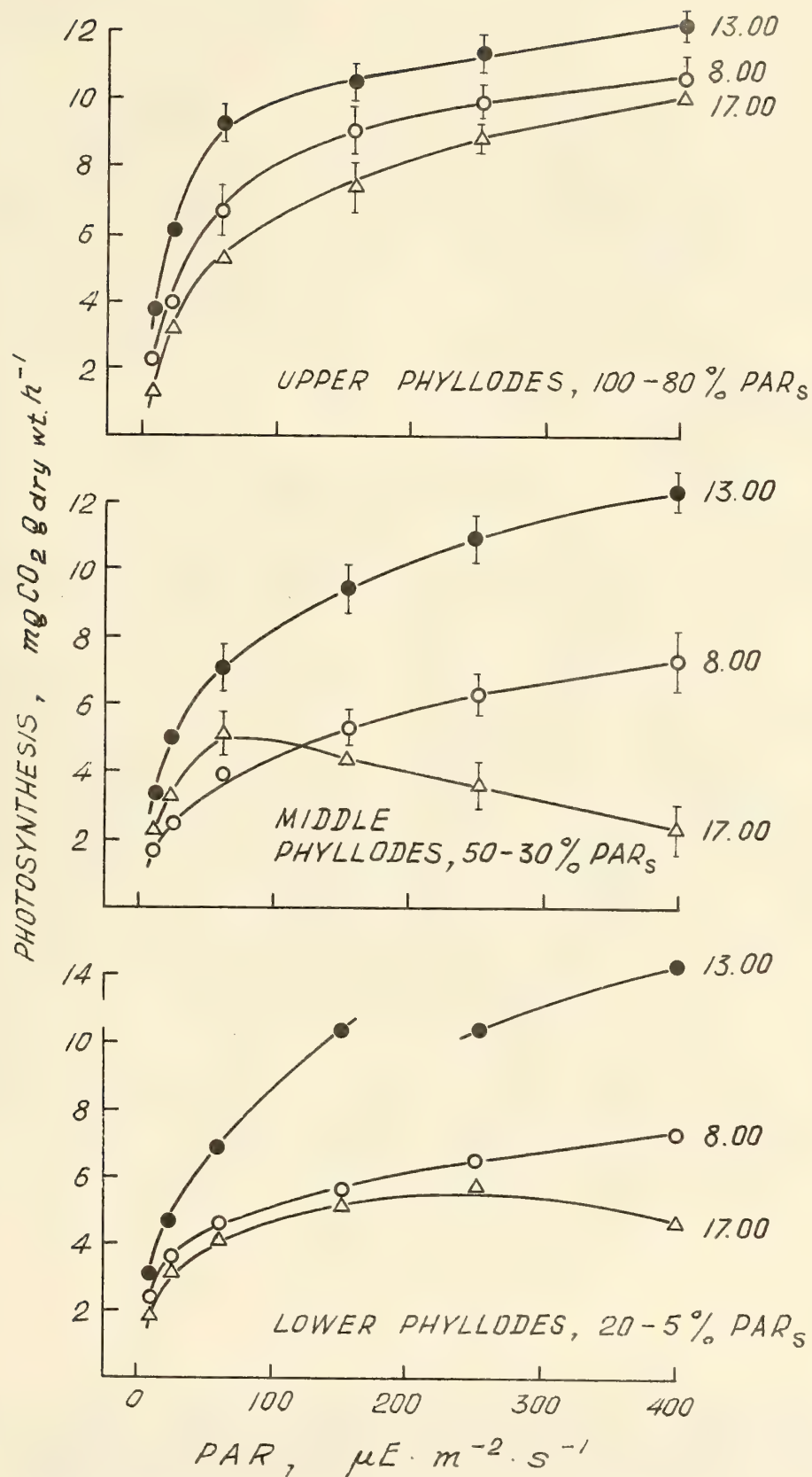


Figure 2. Light dependence of net photosynthesis (P_s vs. I curve) in phylloides of *Sargassum cristaefolium*.

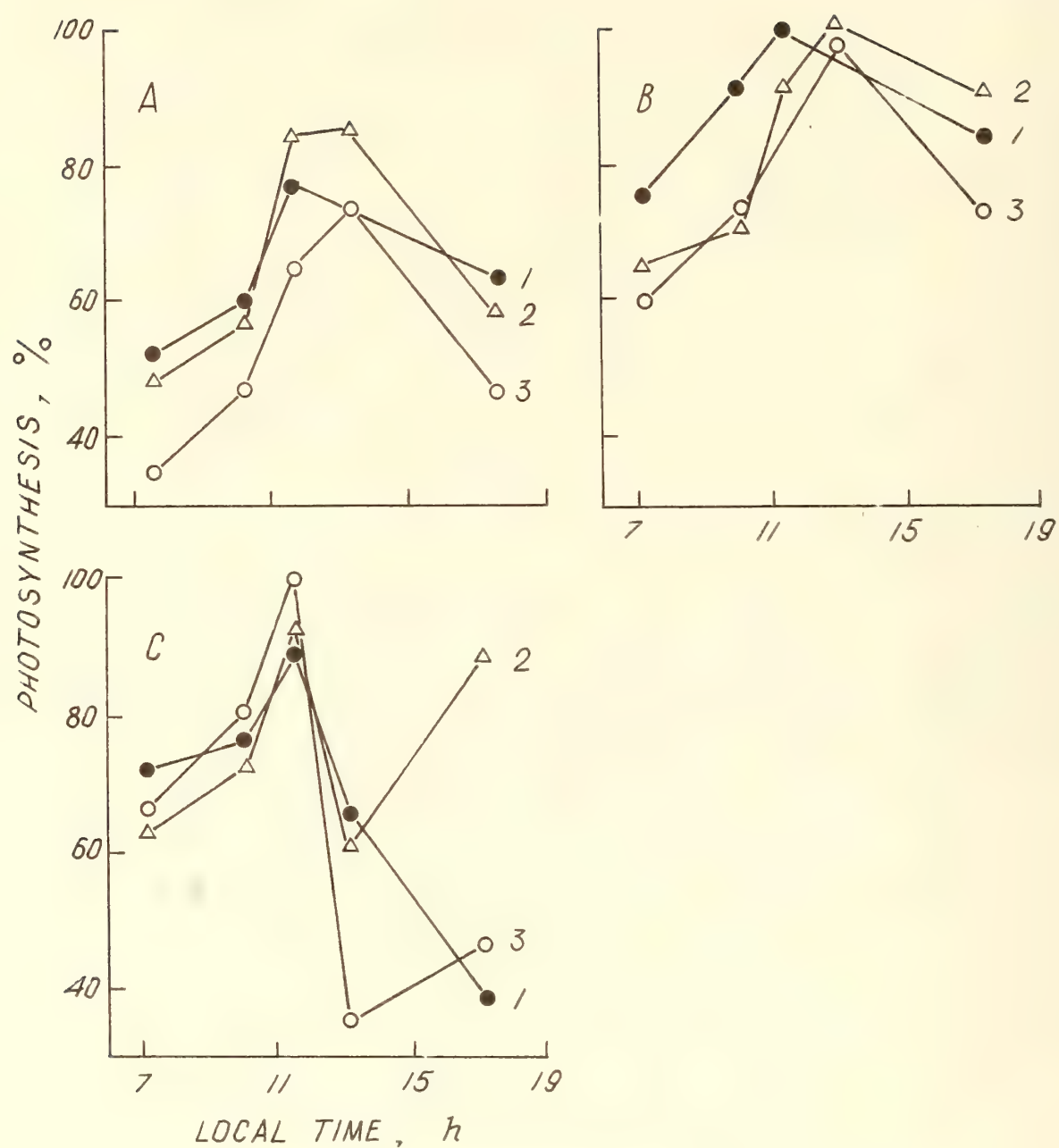


Figure 3. Daily variations of photosynthesis in marine plants. A, measurements at PAR $15 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; B, same at $160 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; C, PAR $380 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. 1, *Thalassodendron ciliatum*, depth 15 m; 2, *Caulerpa* sp., depth 25 m; 3, *Halimeda gracilis*, depth 25 m.

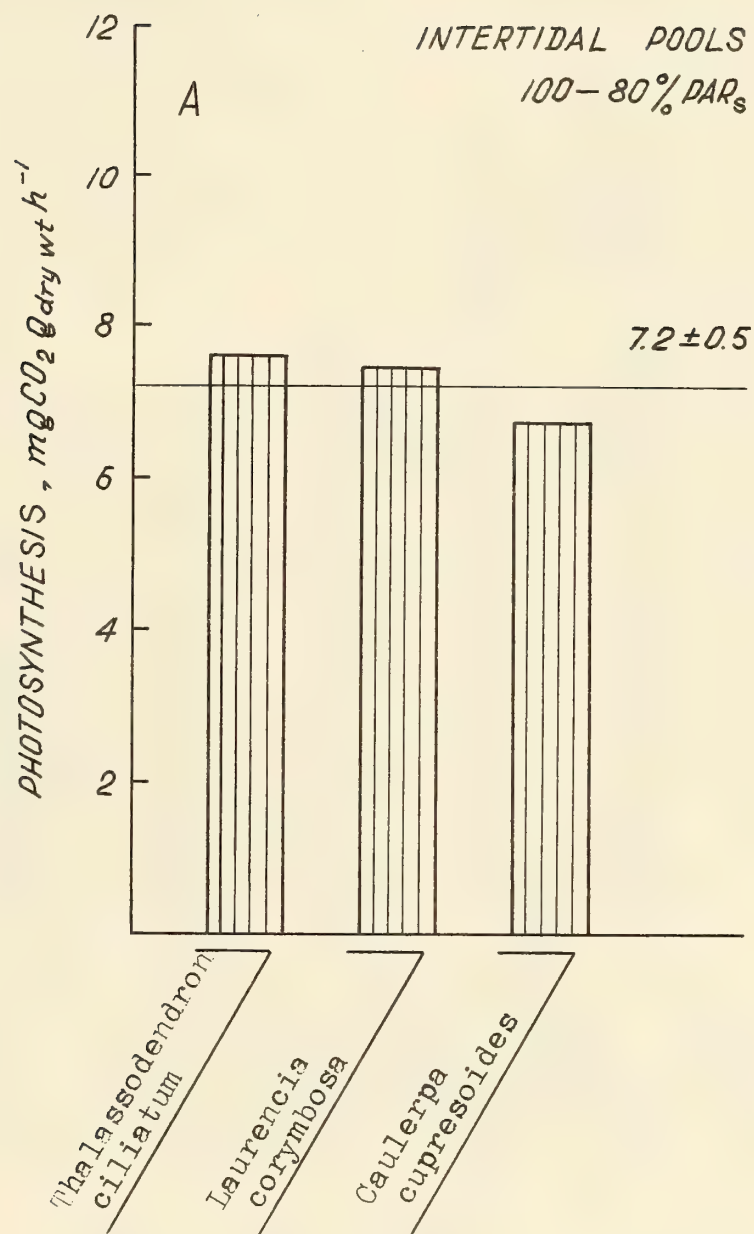


Figure 4 (A). Photosynthetic capacity of marine plants growing at different depths, net photosynthetic light saturation (I_k) in the middle of a sunny day. A - intertidal pools, B, - depth 0.5 - 2 m, C - depth 10 - 15 m, D - depth 20 - 25 m, E - depth 30 - 50 m.

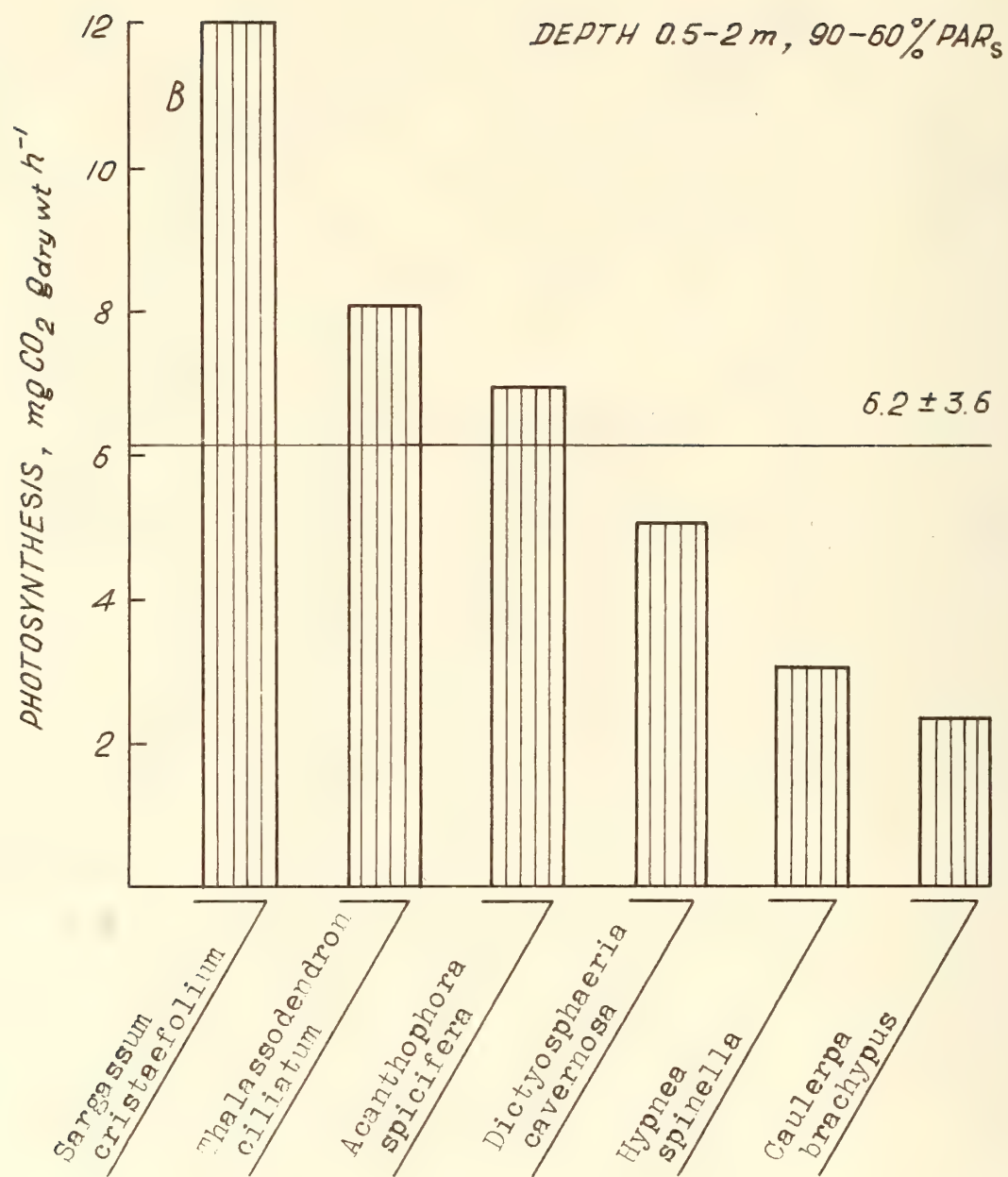


Figure 4 (B).

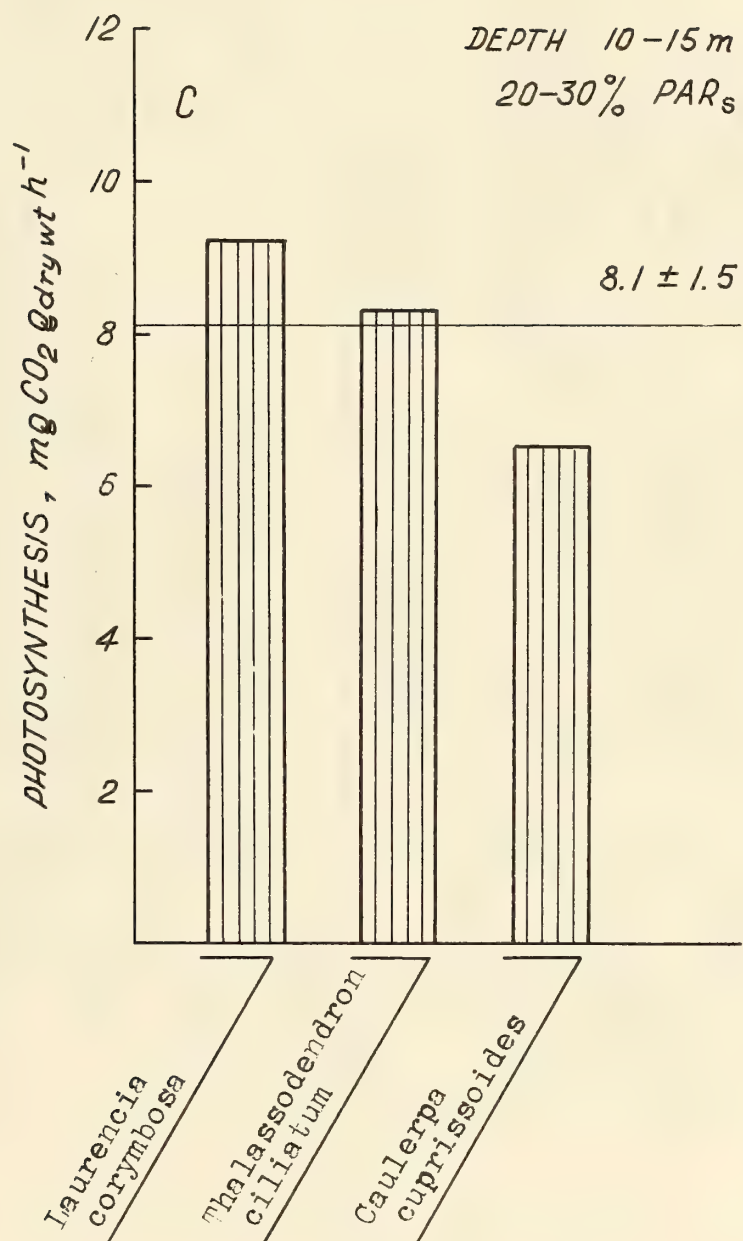


Figure 4 (C).

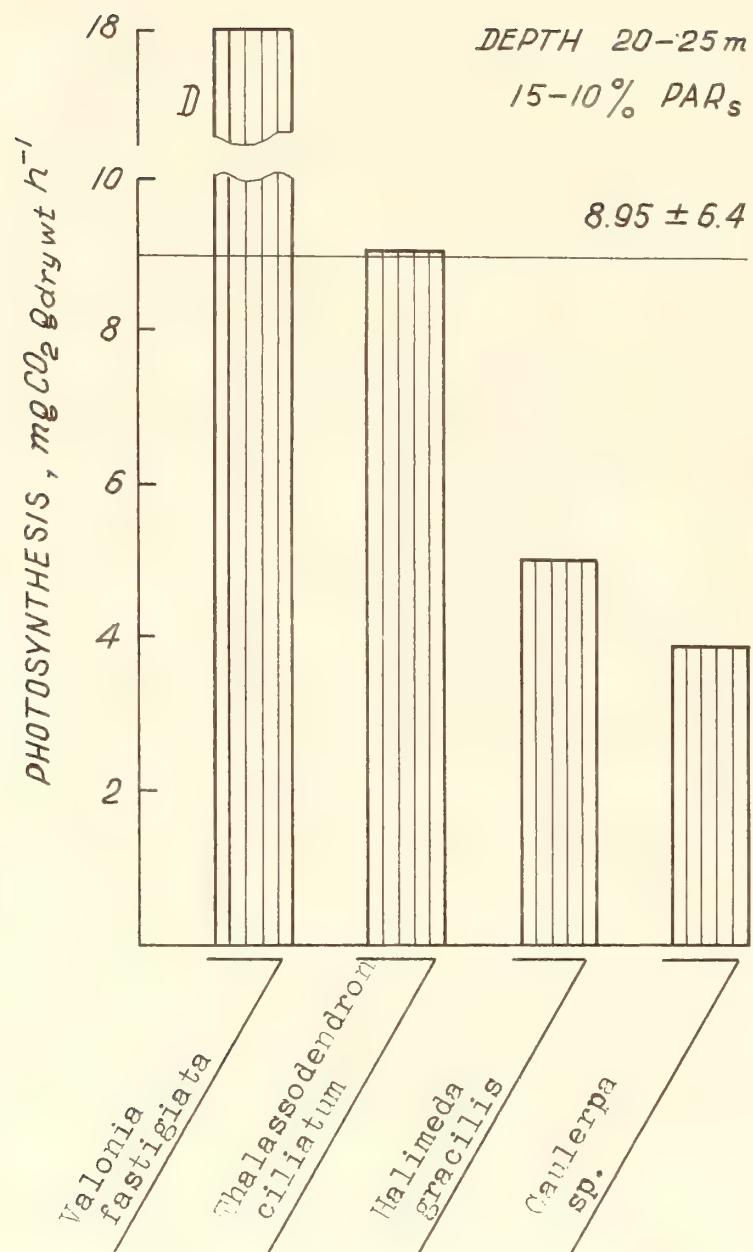


Figure 4 (D).

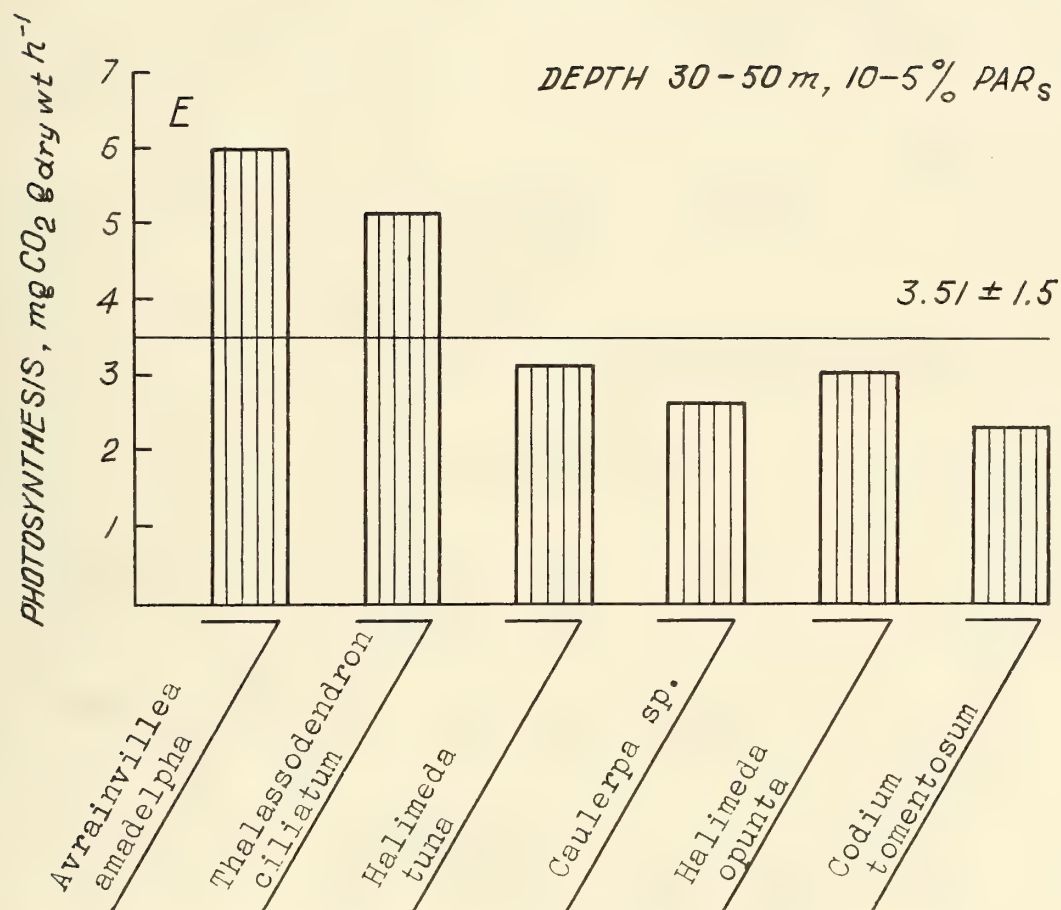


Figure 4 (E).

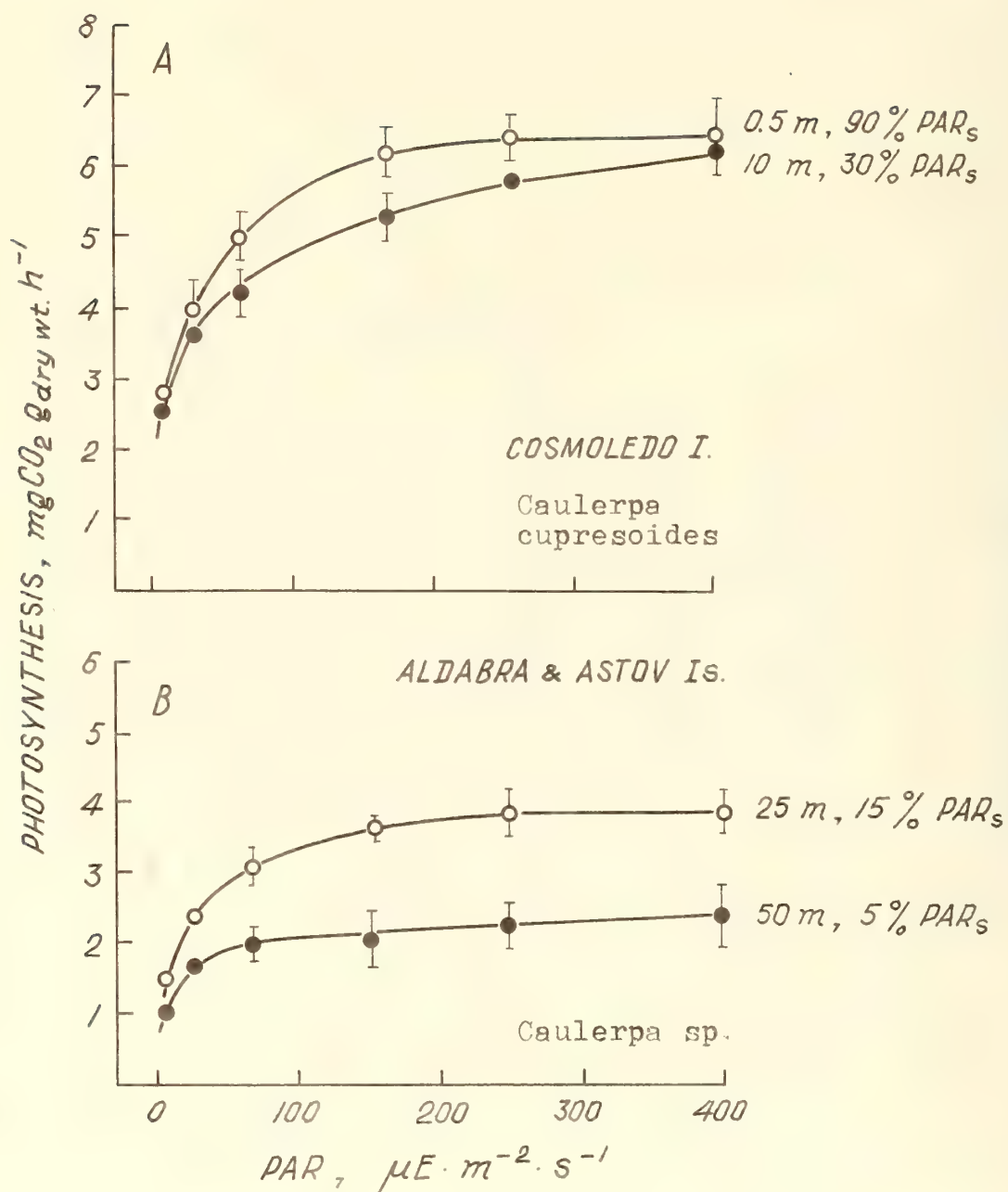


Figure 5 (A, B). Depth-dependence of net photosynthesis in marine plants at 1400 at different depths. A - *Caulerpa cupressoides*, B - *Caulerpa* sp., C - *Thalassodendron ciliatum*, D - *Laurencia corymbosa*.

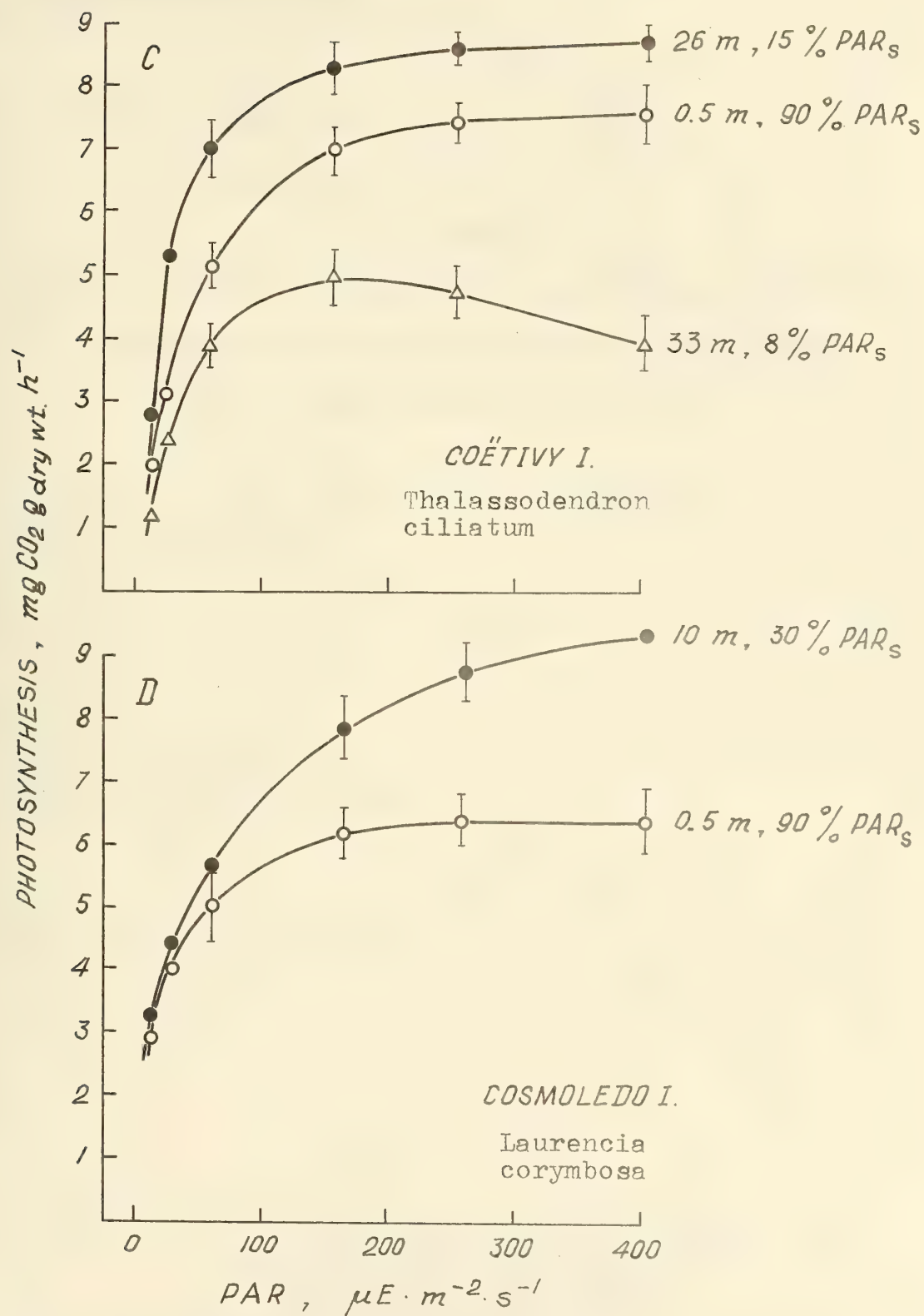


Figure 5 (C, D).

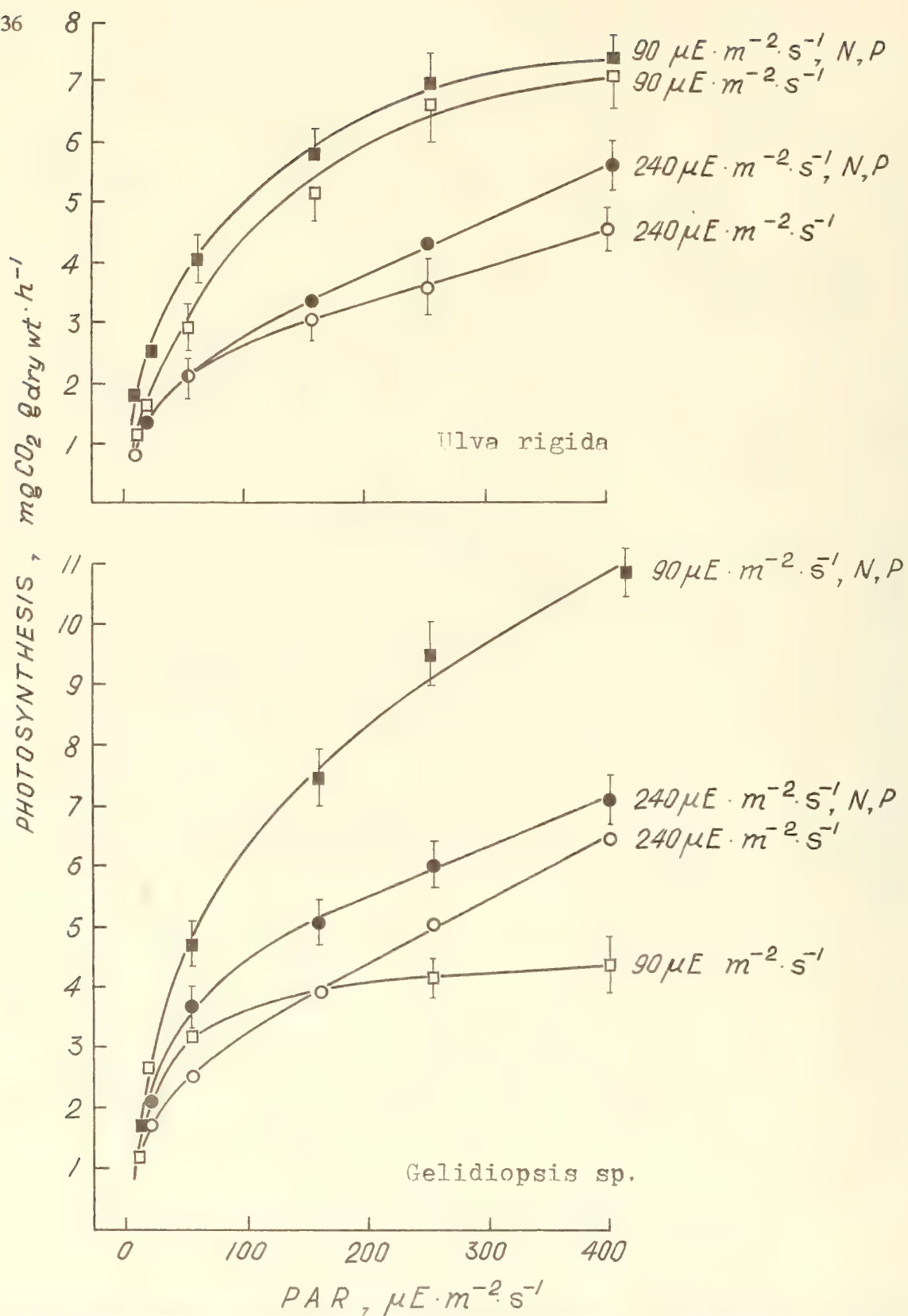


Figure 6. Light dependence of photosynthesis in the experiment on algal adaptation to low light intensity with, or without, addition of dissolved inorganic nutrients. N - 10 mM NH_4Cl ; P - 1 mM KH_2PO_4 .

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CHAPTER 10

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M.M. Littler* and D.S. Littler*

ABSTRACT

The relative nutritional status, with respect to phosphorus (P) versus nitrogen (N) limitation, and light-limited photosynthesis (P_s) was examined over a broad range of quantum fluxes (I) for four species of Chlorophyta (*Codium* sp., *Avrainvillea amadelpha* f. *montagnei*, *Dictyosphaeria cavernosa*, *Udotea orientalis* and two species of Rhodophyta (*Gracilaria crassa*, *G. multifurcata*) taken from Seychelles coastal waters. The results are consistent with the hypothesis that differences in nutrient status among algal forms are related to antecedent habitat history. Maximum photosynthetic rates (P_{max}) for *Codium* sp., *U. orientalis* and *G. multifurcata* from nutrient-poor habitats increased ($P < 0.05$) following nutrient enrichment. However, the species examined from nutrient-rich waters, *A. amadelpha* f. *montagnei*, *D. cavernosa* and *G. crassa*, showed decreases in the initial slope (α) of the P vs. I curve and no significant ($P > 0.05$) increases in P_{max} following nutrient pulses consistent with their previous nutrient environments. The findings suggest that shallow species of tropical macroalgae are adapted to take advantage of episodic nutrient pulses, and that nutrient exposure history can override differences between the various life forms in determining photosynthetic responses to nutrients.

The six shallow water algal species investigated appear well adapted to variable light regimes, including low light conditions. In natural populations of the green alga *A. amadelpha* f. *montagnei*, light-saturated photosynthesis occurred at quite low irradiances ($I_k = 100 \mu E \cdot m^{-2} \cdot s^{-1}$). Associated with low saturation irradiances were low light requirements for photosynthetic compensation ($I_c = 30 \mu E \cdot m^{-2} \cdot s^{-1}$) in this species and reasonably efficient use of low photon flux densities as indicated by a relatively steep slope (α) of the P_s vs. I curve. Conversely, *Codium* sp., *G. crassa* and *G. multifurcata* showed increased photosynthesis as a function of increasing I, with no indication of photoinhibition and relatively shallow α 's.

INTRODUCTION

Large standing stocks of macroalgae on reefs are usually correlated with elevated nutrient supplies (Adey et al. 1977), an observation consistent with the idea that growth rates of tropical reef macroalgae may often be nutrient limited. However, the question of which macronutrient element -- N, P or their interactions -- might limit macroalgal productivity in reef ecosystems has infrequently been addressed experimentally. Traditionally, N is considered the primary limiting nutrient in

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tropical marine waters (e.g., Parsons et al. 1977), although information from geochemical models (Broecker and Peng 1982, Smith 1984) and recent *in situ* macroalgal bioassays (Lapointe 1985, 1987, 1992, Littler et al. 1991) suggests that P may be the more important growth-limiting nutrient in carbonate-rich tropical marine waters. A knowledge of photosynthetic responses to P and N and light by species of tropical reef algae from contrasting habitats could prove useful to clarify current discrepancies (e.g., see Smith 1984) concerning the role of N versus P limitation to algal stocks in tropical marine environments.

Based upon habitat differences in the Seychelles Islands, and the presumed influence of habitat history on nutrient limitation, we hypothesized that different light and nutrient-related responses would be shown by dominant algae from different island environments. To begin to understand the comparative physiological ecology of Seychelles reef algae, we examined the relative nutritional status (N vs P limitation) for four Chlorophyta and two Rhodophyta species. These studies were conducted with manipulations of ambient light levels to test the role of light as an interacting factor with nutrient limitation.

The following specific questions were addressed:

Do macroalgae from enriched waters differ in their relative levels of nutrient limitation from species growing in nutrient-poor habitats?

Is there interaction between nutrients and irradiance in the photosynthetic responses of different species?

Do dark respiration rates (R) and photosynthetic rates at light saturation (P_{max}) vary among species from different habitats?

Do Seychelles Island reef species differ in their light-limited photosynthetic characteristics (α , I_c , I_k).

METHODS AND MATERIALS

This investigation was performed from the research vessel R/V Alexander A. Nesmeyanov throughout the Seychelles Islands from 1 February to 31 March 1989. The specific study sites included St. Joseph Atoll, Pagoda Island of the Cosmoledo Group (a bird island with Guano), and inner and outer harbor sites off the city of Victoria, Mahé Island (Fig. 1). The specimens were held overnight in metal-free, 106-liter, insulated, plastic containers of ambient seawater aboard ship under shaded conditions. Voucher materials of all species were preserved in 4% buffered Formalin and deposited in the Algal Collection, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

On the day prior to photosynthetic assays (i.e., the day of collection), the macroalgae were transported to the R/V Alexander A. Nesmeyanov where they were cleaned of sediments and epiphytes. Subsequently, replicate whole plants of each species were soaked in one of three treatments, a factorial design enrichment of N (NaNO_3) and P (NaH_2PO_4), that consisted of either +N, +P, +N+P or a control (no enrichment). Initial concentrations of N and P in the enrichment were 160 and 16 μM , respectively. The concentrations used were chosen to saturate the uptake rates and represent the upper range of natural levels encountered in highly enriched environments (e.g., bird islands). Following the overnight (12 h) enrichment, the algae were flushed with 3 changes of fresh seawater under shaded conditions (50% I_0) 4 h prior to incubation. Although this enrichment method is based on concepts developed by Smith (1983) for freshwater algae, it has been field tested

previously (Lapointe 1987, Lapointe et al. 1987, Littler et al. 1988) as a macroalgal photosynthetic bioassay, and the results indicated close correlation with longer-term growth responses.

For all productivity (photosynthesis) measurements that followed the 12-h nutrient enrichment period, six replicate incubations per treatment were run. Experimental levels of 7 irradiances and 4 nutrient-pulsed conditions were set up simultaneously in a 7X4 factorial design at ambient water temperatures (27.5-28.4°C) and run between 1000 and 1530 hrs with an average ambient photon-flux density of $2200 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of photosynthetically active radiation (PAR), ranging from a minimum of 1480 to a maximum of $5000 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Incubation chambers were lined with highly reflective aluminum foil to help attain light levels in excess of saturation. Different layers of neutral density screening were used to produce seven experimental light levels (in approximate percent of available sunlight): 100.0%, 50.0%, 25.0%, 12.5%, 3.2%, 0.8% and dark. Photon-flux densities were measured in the field with two integrating 4π sensors (Li Cor Model LI-1000 Data Logger) throughout the incubation periods. Seven layers of neutral density screening and an insulated lid were placed over the 106-liter insulated chamber containing the six incubation jars at the beginning of each run to exclude all light. Incubations were conducted in one liter glass jars that received continuous cooling. Stirring via stir bars on each of the six oxygen electrodes provided vigorous water motion. At five minute intervals, the lid or appropriate layers of screening were removed and dissolved oxygen was recorded at five minute intervals to $0.01 \text{ mg}\cdot\text{l}^{-1}$ with an Orbisphere Model 2610 oxygen analyzer and converted to carbon fixed utilizing respiratory and photosynthetic quotients of 1.00 to facilitate comparisons with other studies. Photosynthesis and respiration were normalized to organic dry weight, which was determined by drying the samples to constant weight at 70°C and ashing them to constant weight at 500°C. The methods concerning selection of material, handling, incubation and oxygen analysis were within the limits recommended by Littler (1979).

Photosynthetic light saturation values (I_k) were obtained for each species at each nutrient level by determining the intersection of a line drawn parallel to the abscissa and through the point of maximum photosynthesis (P_{max}) with the slope of the light-limited P_s vs. I curve (α). The initial slope (α) of each P_s vs. I curve was determined from the least squares linear regression of all productivity values obtained for the linear portion of the curve (i.e., below 12.7 to $50.8 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) including dark respiration (8-18 data points). Compensation irradiances (I_c) were calculated as the intersection of the regression line of the initial P_s vs. I response with the abscissa.

P_{max} values used for statistical comparisons represented the mean of the six greatest photosynthetic values obtained in a particular P_s vs. I curve. Nitrogen and P enrichment effects on P_{max} were assessed by two-way ANOVA and Bonferroni t-test of differences. Significance reported in the results below implies that the probability of the null hypothesis was <0.05 .

RESULTS

Maximum net apparent photosynthesis (P_{max}) in *Codium* sp. from the pristine St. Joseph Atoll (Table 1, Fig. 2) was strongly N-limited (N significantly greater than control, $P<0.05$). Values of samples pulsed with P were consistently higher than the controls but not to a statistically significant degree ($P>0.05$). The two nutrients combined produced a significant ($P<0.05$) synergistic increase in net apparent photosynthesis. Net photosynthesis began to show light saturation (I_k) above about $I_k=250 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the controls and at lower light levels ($150\text{--}170 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in the pulsed samples (Table 1). The nutrient-pulsed material had compensation intensities (I_c , Table 1) that were all less than half that of the controls ($80 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The α values of the pulsed material were consistently higher than that of the control samples (Table 1).

For *Udotea orientalis* from another pristine environment on St. Joseph Atoll, P_{\max} significantly increased ($P < 0.05$) following pulses of N or P, but no P + N synergism occurred (Fig. 3, Table 1). Net apparent photosynthesis became light saturated at around $170\text{--}280 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (I_k) in the control and N-pulsed samples but was substantially higher ($410 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in the samples pulsed with P alone (Table 1). The nutrient-pulsed samples showed somewhat lower I_c values than the controls, particularly in the case of the N-pulsed material (30 vs. $140 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Table 1). The α values were similar with the exception of the P-pulsed material which was two to three times lower (Table 1).

In *Avrainvillea amadelpha* f. *montagnei* (Fig. 4, Table 1), from the guano-influenced Pagoda Island, Cosmoledo Atoll, there was no significant ($P > 0.05$) change in P_{\max} for any of the pulsed treatments. Net photosynthesis began to show light saturation at the relatively low I_k of $100 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in the controls and at 310, 354 and $633 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for N-, P- and N+P-pulsed material, respectively (Table 1). I_c values followed this same trend with lower control values and a much higher I_c in the N+P-pulsed samples. The α values of the nutrient enriched materials were substantially lower, particularly in the case of the N+P-pulsed material, than in the controls (Table 1).

Dictyosphaeria cavernosa, the dominant alga from Pagode Island (Fig. 5), Cosmoledo Atoll, under the direct influence of seabird guano, showed no significant ($P > 0.05$) nutrient stimulation of P_{\max} , with substantial inhibition in the P- and N+P-pulsed samples (Table 1). Net photosynthesis tended to become light saturated at $320\text{--}370 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, except in the case of the N-pulsed samples ($I_k = 540 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The nutrient-pulsed material had slightly elevated I_c values than the controls (Table 1). The α values, conversely, were nearly twice as high in the controls as in the pulsed material.

Gracilaria multifurcata from Cerf Island outside of Victoria Harbor, Mahe (Fig. 6), had P_{\max} stimulated most by pulses of P (significant at $P < 0.05$) and to a lesser degree by N and N+P. Light saturation of the control (Table 1) was somewhat high compared to the other algal species, as reflected by an I_k of $480 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The nutrient-pulsed samples showed quite high I_k values ranging from 510 to $870 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Only the N-pulsed samples had substantially higher I_c values than the controls (120 vs. $70 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Table 1).

In *Gracilaria crassa* (Fig. 7), a dominant in the highly eutrophic shallow waters adjacent to the shoreline of Victoria Harbor, Mahe, all combinations of additions of N, P, or both, significantly ($P < 0.05$) inhibited P_{\max} . Light saturation began to appear earlier in the controls, with an I_k of $380 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ compared with $1200\text{--}1975 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the pulsed samples. Correspondingly, the new compensation value was much lower for the controls, which had an I_c of 60 compared with $280\text{--}400 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the pulsed material. Concomitantly, the pulsed samples showed substantially reduced α values compared with the untreated controls (Table 1).

There was a tendency for respiration (R) to decrease following nutrient pulses in most species. However, statistically significant ($P < 0.05$) declines in R were shown only for the pulsed samples of *Udotea orientalis* from St. Joseph Atoll (Table 1).

DISCUSSION

McRoy and Lloyd (1981) have categorized marine macrophytes as comprising two fundamentally different groups: (1) the macroalgae and (2) the seagrasses. The former group, as characterized by these authors, is analogous to filter-feeding animals in terms of extraction of nutrients from the seawater milieu, while secured to two-dimensional substrata by means of a holdfast. Members of the latter group extract nutrients from both the water column and pore waters of the soft, sedimentary,

three-dimensional substrata by means of vascular root-rhizoid systems that also serve for anchoring them. This dichotomy overlooks many siphonaceous algae (=rhizophytes), such as *Udotea orientalis*, prevalent in habitats characterized by sedimentary substrata. Such algae, mainly of the order Bryopsidales, anchored in nutrient-laden pore waters (Littler and Littler 1990), also have extensive root-like and rhizomatous systems for attachment in soft substrata and, because cross walls are minimal, these plants can utilize active transport, rapid turnover and cytoplasmic streaming to translocate nutrients taken up from both the sedimentary pore waters and water column milieu (Williams 1984). *Udotea orientalis* (Fig. 3) did not support the finding of Littler and Littler (1990) that psammophytic rhizophytes tend to exhibit little response to the overall P_s vs. I relationship following nutrient pulses. However, the sedimentary substratum from which this psammophyte was taken on St. Joseph Atoll is especially white aerobic sand free of pigmented organic or other matter. This finding is in agreement with the two epilithic forms, *Codium* sp. and *Gracilaria multifurcata* (Figs. 2 and 5), also from low nutrient waters, where the same result prevailed; i.e., a trend towards overall increases in the nutrient pulsed samples relative to unpulsed control material.

Contrastingly, P_{max} in the two epilithic forms (haptophytes), *Halimeda lacrimosa* and *Halimeda copiosa* from the Bahamas (Littler et al. 1988), increased consistently in thalli which had been pulsed with N, whereas P was inhibitory ($P < 0.05$). Conversely, treatment with P resulted in higher P_{max} in both of the psammophytic *Halimeda* species investigated, ($P < 0.05$), suggesting (Littler et al. 1988) that epilithic and psammophytic *Halimeda* species may tend to differ in their nutrient status with regard to N and P requirements. The P-limitation previously observed in psammophytic species corresponds with the observed high N:P ratios of sediment pore waters in carbonate-rich sediments (Rosenfeld 1979; Berner 1974), which could result in the P-limited state Littler et al. (1988) observed. Alternatively, epilithic forms, which must rely more on water-column N and P availability, appear (Littler and Littler 1990) to be more N-limited, possibly because of lower N:P ratios characteristic of shallow tropical waters. In contrast, our data for *U. orientalis*, a rhizophyte from an exceptionally pristine sedimentary environment, did not show differential P vs. N limitation (Fig. 3).

The demonstration of the P-limited nutrient condition for *Gracilaria multifurcata* also differs from the above and from studies in the coastal marine environment along eastern North America where N was considered the primary nutrient limiting growth of both phytoplankton (Ryther and Dunstan 1971, Vince and Valiela 1973) and macroalgae (Topinka and Robbins 1976, Chapman and Craigie 1977, Hanisak 1979). However, nutrient bioassays along Florida's northern Gulf coast have shown that P is frequently more important than N in regulating phytoplankton productivity (Myers and Iverson 1981). Several recent macroalgal studies (Lapointe 1985, 1986, 1987, Littler et al. 1988, Littler and Littler 1990) also showed P limitation in tropical macroalgae. This supports the opinion held by geochemists (Broecker and Peng 1982, Smith 1984) and, in particular, Redfield (1958) that the oceans as a whole are P-limited ecosystems. In contrast, our data for *Codium* sp., agree with those for other epilithic algae (see Topinka and Robbins 1976, Chapman and Craigie 1977, Hanisak 1979) and for a similar rock grower, *Halimeda opuntia*, from Belize, which also demonstrated (Lapointe et al. 1987) photosynthetic enhancement only by N enrichment.

In most cases, exposure to nutrient pulses that increased P_{max} tended to decrease R (Table 1). This observation is inconsistent with the idea that R is elevated when short-term pulses of nutrient enrichment are quickly metabolized into photosynthetic and respiratory machinery, as found in experimental studies with other macroalgae (Lapointe et al. 1984). An increased R normally is attributable to increased metabolic cost associated with energetic requirements for nutrient uptake across membrane surfaces, as originally shown by Syrett (1953), or to increased P_{max} machinery, as evidenced during sun/shade acclimation.

Although the light environment is generally acknowledged as an important ecological factor in the distributions and abundances of marine algae (e.g., Ramus 1981, Mazzella and Alberte 1986),

comprehensive information for tropical whole-algal photosynthetic attributes such as rates of maximum light-saturated photosynthesis, compensation irradiance, saturation irradiance, the initial slope of the photosynthesis-irradiance curve and dark respiration is available only for a several species of *Halimeda* (Littler et al. 1988). Thalli of shallow *Halimeda* species in clear tropical waters often exhibit light-saturated photosynthesis at irradiances that are much lower than levels available on typical sunny days. With a measured light attenuation for clear Seychelles waters of about 0.4% of photosynthetically active surface irradiance per meter of depth, the deepest specimens we collected (7-m deep) would have been growing in up to 97% of the light energy available at the surface. Our results indicate photosynthesis in some shallow tropical macroalgae can reach a maximum under relatively low light energies and that many species appear well adapted to variable light regimes, including low-light conditions, as particularly illustrated by *Avrainvillea amadelpha* f. *montagnei* (Fig. 4). Concomitant with low saturation irradiances are low light requirements for photosynthetic compensation and reasonably efficient use of low photon flux densities as indicated by the steep slopes of the P_s vs. I curves. Of the six species we studied, *A. amadelpha* f. *montagnei* clearly emerges as the most shade adapted, with considerably higher α values and relatively low I_c and I_k values.

In comparison to our data, five uncalcified temperate chlorophyta (Arnold and Murray 1980) had initial P_s vs. I slopes (α) that ranged from 0.018 mg C·g dry wt⁻¹·h⁻¹ per $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the thick optically dense alga *Codium fragile* (Sur.) Har. to 0.129 for the thin sheet-like *Ulva Rigida* C. Ag. Our α values for untreated material ranged from 0.012 mg C·g ODW⁻¹·h⁻¹ per $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to 0.034. In other words, the full range found for selected genera was exceeded within this small study group of six taxa. *Codium* sp. increased markedly in α following pulses of nutrients, whereas the other species tended to show lower α values following pulses of either nutrient or both. Arnold and Murray (1980) recorded compensation intensities ranging from 6.1 to 11.4 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and saturation intensities from 50.3 to 81.9 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for five temperate chlorophytes; all were photoinhibited in full sunlight. In comparison, the ranges we obtained for untreated Seychelles algae were considerably higher (e.g., I_c from 30 to 140 and I_k from 100 to 480).

Previously published net photosynthetic rates for other tropical species (i.e., *Halimeda*, Littler and Littler 1990) have ranged from 0.8 to 6.4 mg C·g organic dry wt⁻¹·h⁻¹, with a mean of 2.1 mg C·g ODW⁻¹·h⁻¹. This is comparable to the mean of 3.5 and range of 1.3 to 4.6 mg C·g ODW⁻¹·h⁻¹ determined for untreated controls of the six species investigated here. Our highest rates of photosynthesis did not necessarily come from thalli previously exposed to high nutrient levels. Other published values (see Littler et al. 1986b) for common tropical macroalgal species incubated in full ambient irradiances range from 0.3 mg C·g ODW⁻¹·h⁻¹ for crustose forms to 13.4 mg C·g ODW⁻¹·h⁻¹ for thin frondose forms.

In a parallel exploratory study, Littler et al. (1991) characterized some of the environmental features of the same habitats studied here and the reader is referred to that work for detail. Seawater nutrient samples were taken at midday next to the algal thalli used in the photosynthesis/nutrient assays reported here. Total inorganic nitrogen was lowest at St. Joseph Atoll (0.64 μM) followed by Victoria Harbor (0.77), Cerf Island (1.29) and the guano enriched Pagode Island, with a very high level of 5.48 μM (Littler et al. 1991). Orthophosphate levels followed the same trend with the lowest total inorganic phosphorus at St. Joseph Atoll (0.11 μM) followed by Cerf Island (0.12), Victoria Harbor (0.22) and Pagode Island (with the highest value of 0.50 μM). Novozhilov et al. (1992) also noted that the waters of Victoria Harbor and near the bird rookeries of Cosmoledo Atoll contain elevated levels of nutrients which they likewise attributed to sewage discharges and bird excrements, respectively. Our photosynthetic assays coincide closely with the predicted trends in nutrient levels and are consistent with the hypothesis that macroalgae from enriched waters differ in their relative levels of nutrient limitation from species growing in nutrient-poor habitats. This finding is in agreement with more extensive bioassay studies for tropical macroalgae (see Littler et al. 1991,

Lapointe et al. 1992). It appears that tropical macroalgae are not only adapted to large variations in the light environment, but can take advantage of episodic nutrient pulses, possibly such as those documented for temperate kelp forests (Zimmerman and Kremer 1984) and tropical photosynthetic corals (Meyer et al. 1983).

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Table 1. Photosynthetic and dark respiratory characteristics in relation to various nutrient conditions (α = mg C·g organic dry weight (ODW)⁻¹·h⁻¹ per $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Asterisks indicate values that are significantly different for only P_{max} and R (* = $P < 0.05$, ANOVA using Bonferroni t tests of differences) from the controls. The α , I_c and I_k values were time-series dependent and not analyzed statistically.

Species and treatment	P _{max}	R	α	I _c	I _k
	(mg C·gODW ⁻¹ ·h ⁻¹)			(μE·m ⁻² ·s ⁻¹)	
<i>Codium</i> sp.					
Control	3.18±.097	-1.93±0.64	0.021	80	250
+Nitrogen	6.51±1.97*	-2.21±1.68	0.052	37	150
+Phosphorus	4.40±0.38	-1.07±0.43	0.032	20	150
+N+P	4.80±0.36*	-1.25±0.32	0.038	23	170
<i>Udotea orientalis</i>					
Control	1.31±0.42	-3.53±1.36	0.018	140	220
+Nitrogen	3.23±0.92*	-1.51±0.32*	0.021	30	170
+Phosphorus	2.50±0.57*	-1.56±0.30*	0.007	80	410
+N+P	2.09±0.30	-1.66±0.70*	0.013	120	280
<i>Avrainvillea amadelpha</i> f. <i>montagnei</i>					
Control	2.56±0.55	-1.62±1.29	0.034	30	100
+Nitrogen	3.15±0.56	-0.82±0.13	0.012	50	310
+Phosphorus	3.24±0.33	-0.92±0.18	0.010	64	354
+N+P	2.53±0.49	-0.94±0.11	0.006	148	633
<i>Dictyosphaeria cavernosa</i>					
Control	4.09±1.46	-3.87±2.61	0.021	140	320
+Nitrogen	4.43±0.24	-2.20±0.98	0.012	165	540
+Phosphorus	2.63±1.45	-3.51±2.82	0.014	170	350
+N+P	3.24±1.03	-3.33±0.91	0.011	150	370
<i>Gracilaria multifurcata</i>					
Control	5.06±0.59	-0.89±0.26	0.012	70	480
+Nitrogen	5.43±0.88	-0.73±0.41	0.006	120	870
+Phosphorus	6.55±0.78*	-0.75±0.05	0.015	60	510
+N+P	6.07±0.79	-0.55±0.08	0.008	40	750
<i>Gracilaria crassa</i>					
Control	4.56±0.78	-0.88±0.19	0.014	60	380
+Nitrogen	3.42±0.66*	-1.15±0.40	0.003	400	1300
+Phosphorus	3.15±0.90*	-1.02±0.20	0.002	280	1975
+N+P	3.57±0.65*	-0.88±0.28	0.004	280	1200

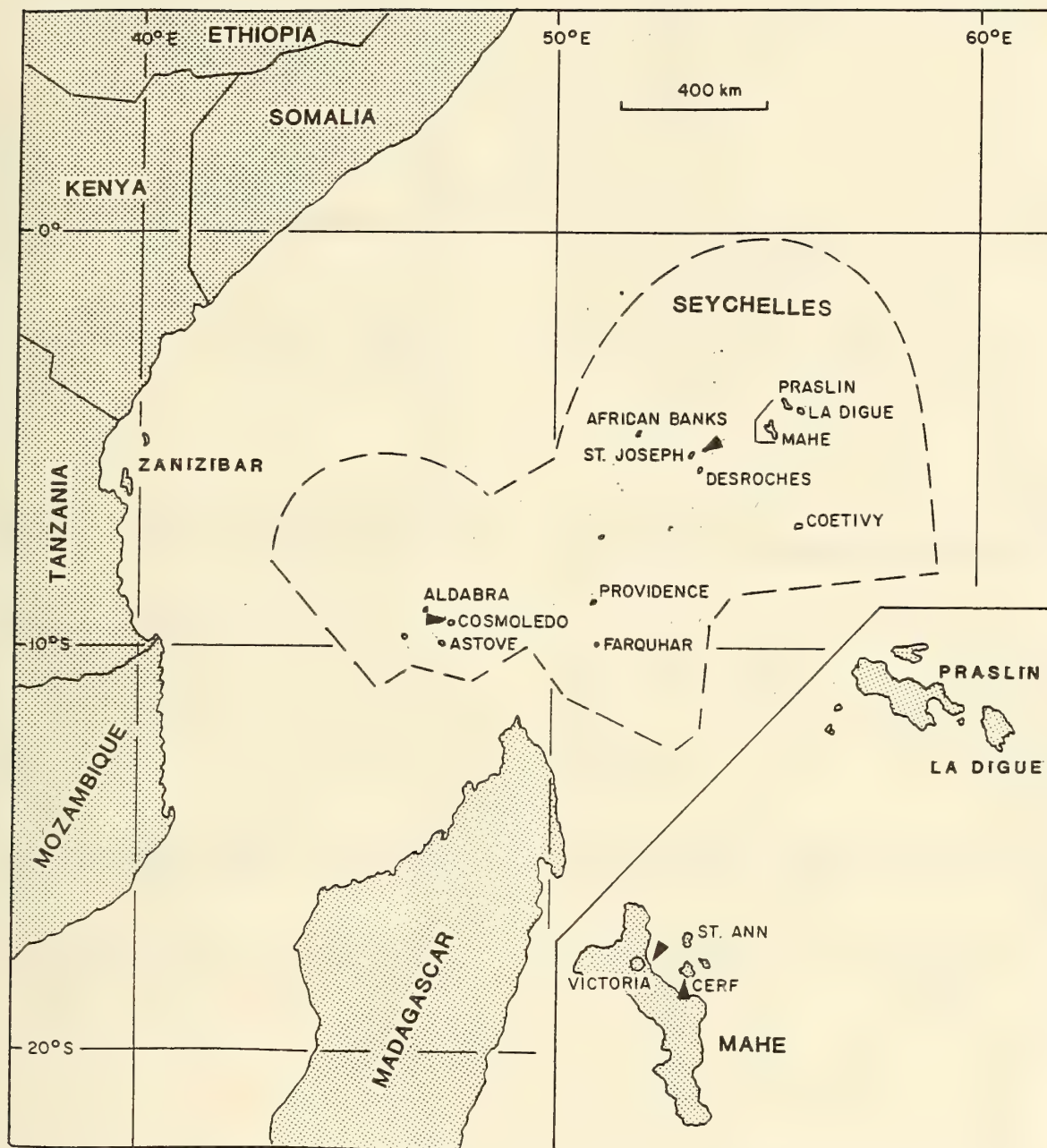


Figure 1. Map showing the locations (arrows) of the four study areas. The collection sites on St. Joseph Atoll and Cerf Island are relatively oligotrophic compared to the eutrophic sites on the guano-influenced Pagoda Island, Cosmoledo Atoll, and the sewage-influenced Victoria Harbor, Mahé. Inset shows the group of granitic islands in larger detail.

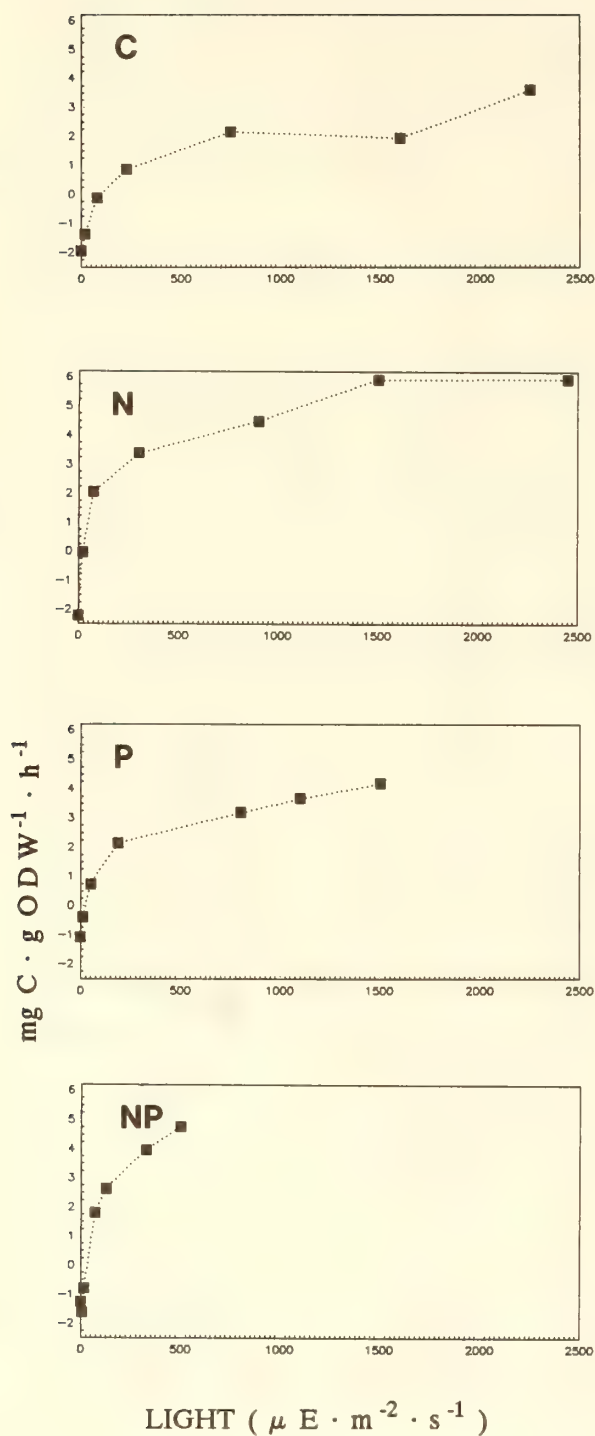


Figure 2. P_s versus I response of *Codium* sp. in relation to four nutrient treatments. (C) Control (no nutrients added), (N) Nitrogen (NaNO_3) added, (P) Phosphorous (NaH_2PO_4) added and (NP) Both N and P added.

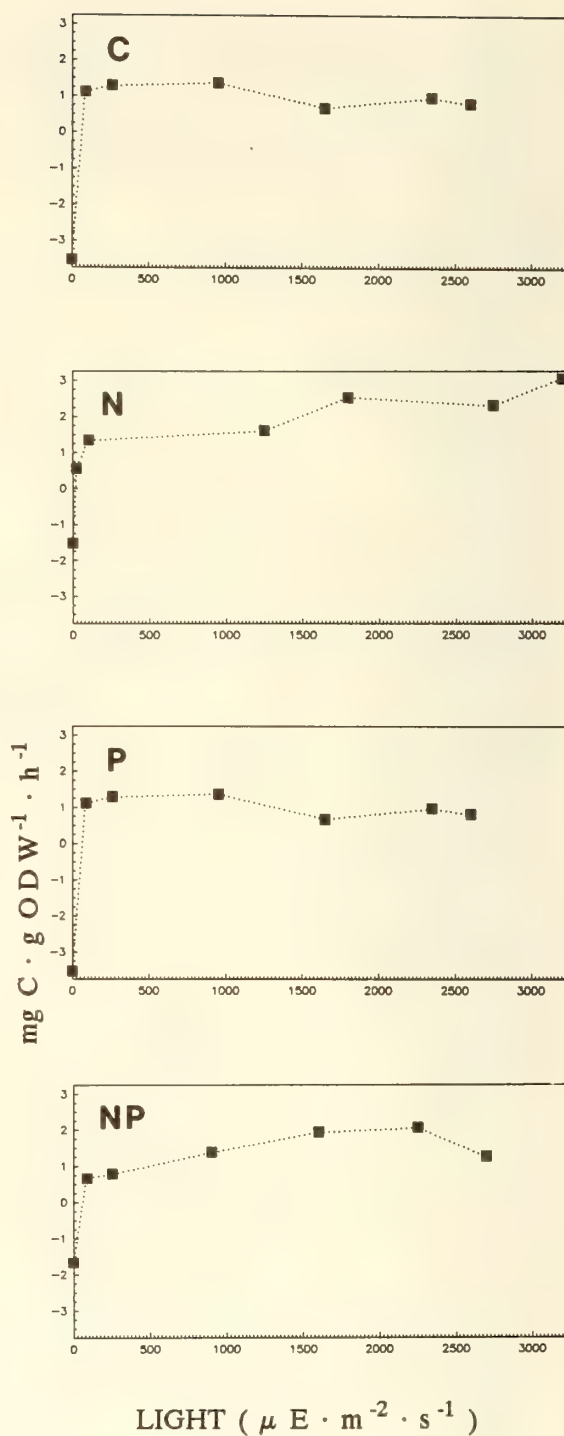


Figure 3. P_s versus I responses of *Udotea orientalis* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

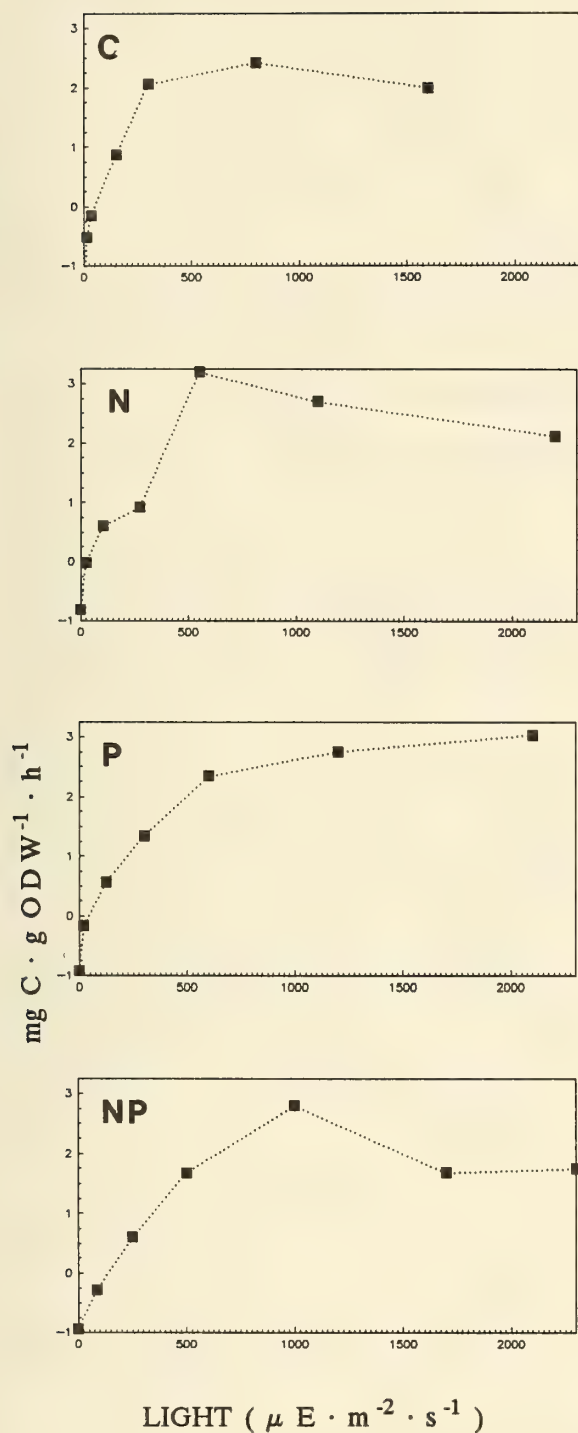


Figure 4. P_s versus I responses of *Avrainvillea amadelpha* f. *montagnei* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

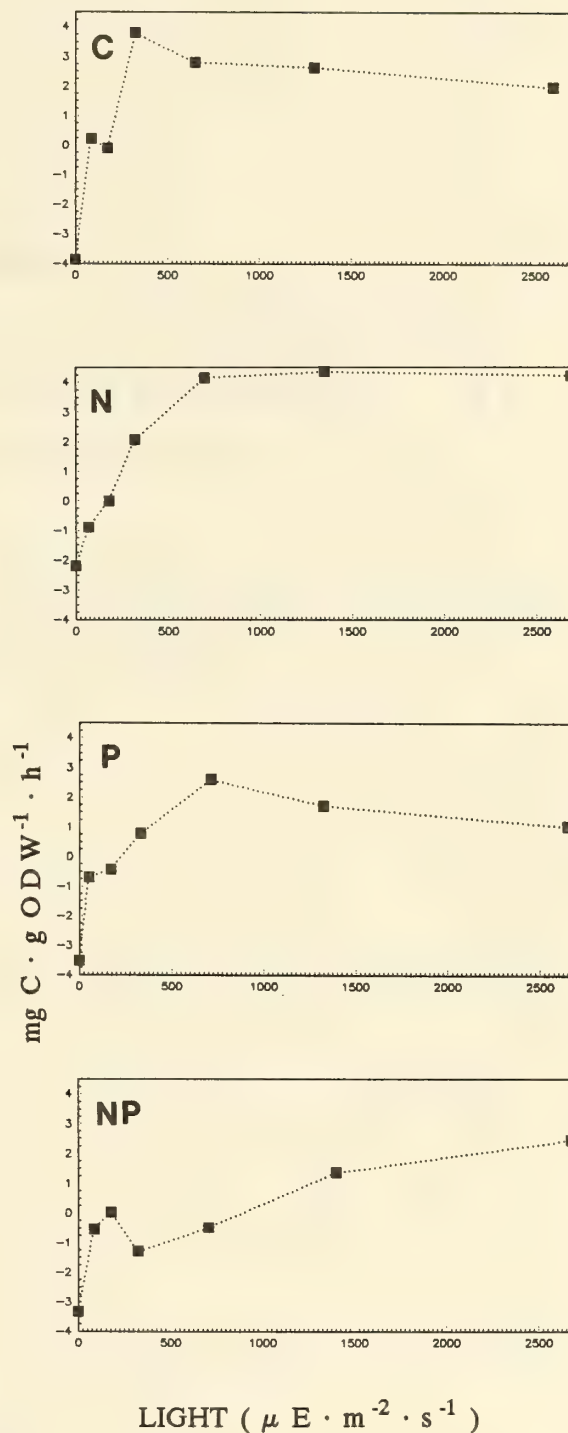


Figure 5. P_s versus I responses of *Dictyosphaeria cavernosa* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

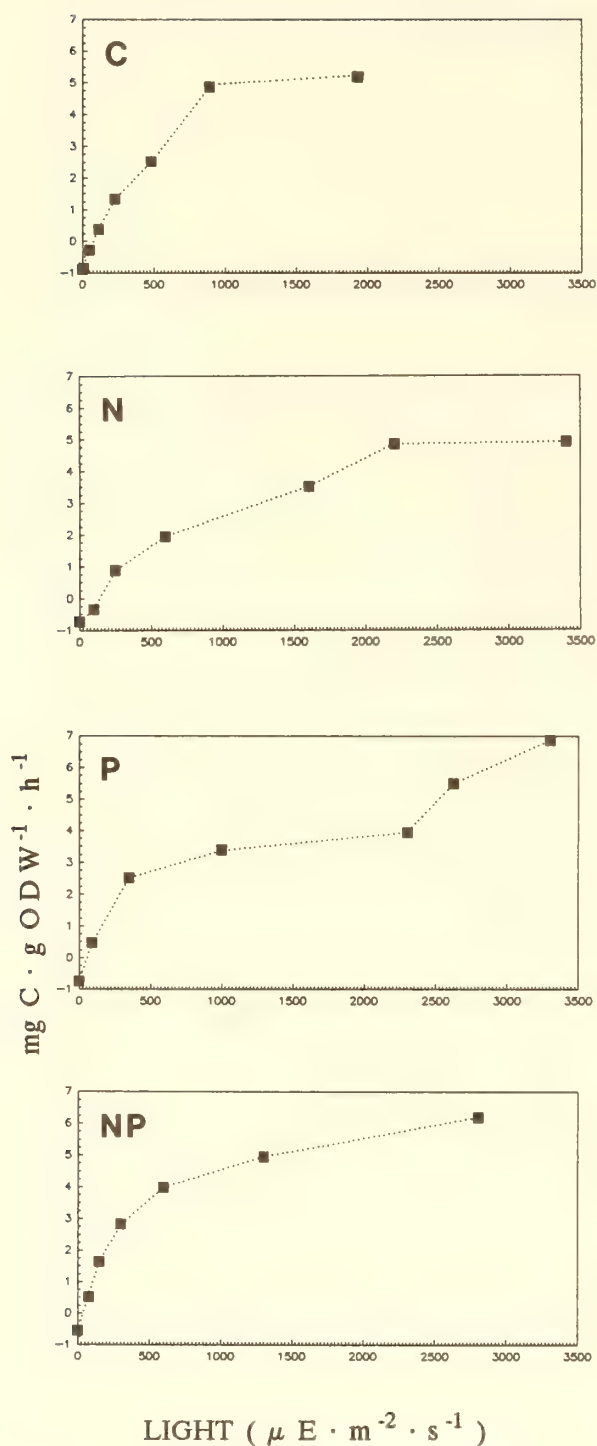


Figure 6. P_s versus I responses of *Gracilaria multifurcata* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

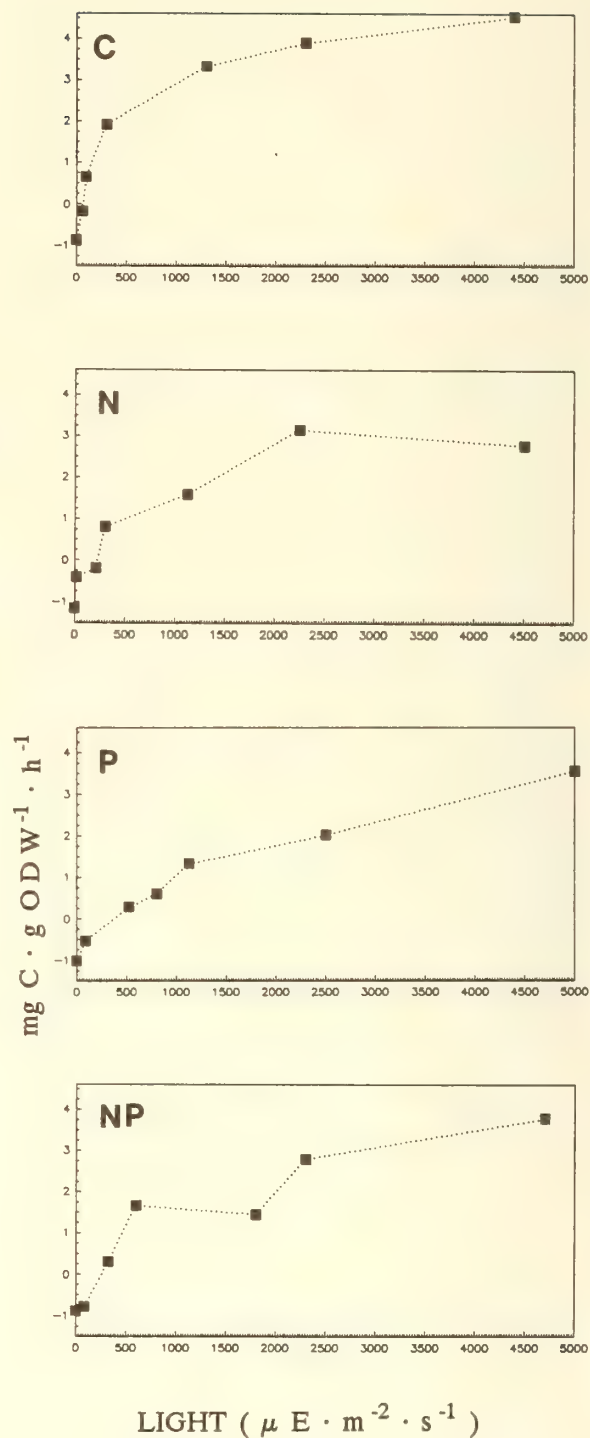


Figure 7. P_s versus I responses of *Gracilaria crassa* in relation to four levels of nutrients. Features are the same as those indicated in Fig. 1.

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CHAPTER 11

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CARBON ASSIMILATION AND PRIMARY PRODUCTION IN
THALASSODENDRON CILIATUM BLADES

BY

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E.A. Titlyanov^{*}, V.A. Leletkin^{*}, K.Y. Bil^{**}, P.V. Kolmakov^{*} and E.G. Nechai^{*}

INTRODUCTION

Seagrasses play an important role in coastal ecosystems, serving as a food source and habitat for numerous animals as well as stabilizing sediments and forming biotopes (Stephes 1968, den Hartog 1970, Bjorndal 1980, Sheridan and Livingston 1983). Despite the low diversity of seagrasses in the world ocean (only 50 species, Lakshman 1985, Dawes 1987), they can be found in all geographical zones occupying depths from 0 to 40 m. Seagrasses are especially abundant near river estuaries and reef lagoons where they are often the dominant autotrophic producers. For example, the standing crop of *Thalassia testudinum* in Bear Cut produces 2750 g dry wt·m⁻² a year (Jones 1968) and *T. testudinum* from Boca Ciega Bay, Florida, 1198 g dry wt·m⁻² (Taylor and Saloman 1968).

Thalassodendron ciliatum (Försk) den Hartog also displays high productivity: up to 2 kg C·m⁻²·yr⁻¹ (Harves 1982, Aleem 1984, Thorhaug 1986). In favorable seasons, the growth rate of some species can be very high and the rate of blade elongation can reach 1 - 1.5 cm·day⁻¹ (Greenway 1974, Johnstone 1979). The blade growth of *Halodule wrightii* Ascherson from the Indian River, Florida, during the spring is 11% per day (Virstein 1982).

Physiological studies have been widely conducted on the production capacities of separate plants, associations of seagrasses and their epiphytes and the effects of environmental factors on photosynthesis, growth and development (Backman and Barilotti 1976, McRoy and McMillan 1977, Weigert 1979, Harlin 1980, Montfrans et al. 1984, Dennison and Alberte 1982, 1985). *Zostera marina* and *Thalassia testudinum* are the most widely studied of all seagrasses. In a number of investigations, seagrasses were successfully cultivated (Lakshmanan 1985, Thorhaug 1986).

The goal of this work was to study the light dependence of oxygen evolution and carbon assimilation during photosynthesis, as well as the temperature dependence of oxygen exchange in *Thalassodendron ciliatum* blades from 0-33 m in depth. Using the data obtained, net primary production of the seagrass was calculated for both clear and turbid waters of the Seychelles Islands.

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MATERIALS AND METHODS

The study was carried out during the expedition of the R/V Akademik A. Nesmeyanov to the Seychelles Islands during January - March 1989. The seagrass *Thalassodendron ciliatum* (Forsk) den Hartog which grew in abundance on C  tivy, Farquhar, Aldabra and Desroches Islands at depths of 0-37 m was chosen as the subject for study. C  tivy Island was especially convenient for a comparative study since vast growths of *T. ciliatum* occurred there at all depths to 37 m, both on the inside of the lagoon and on the outer reef slope.

We studied young, mature and old blades of the leaf cluster. The leaf cluster of *Thalassodendron ciliatum* can be subdivided into two equal portions which are mirror images of each other. The young blades included the 1st and 2nd blades of every half of a given leaf cluster, the 3rd and 4th blades were referred to as mature blades, and the 5th blade was designated as an old blade.

Daily photosynthetic production was calculated on the basis of measurements of light and temperature dependence of oxygen exchange of *Thalassodendron ciliatum* blades and their comparison with values of habitat illumination and temperature at 0, 2, 15, and 33 m depths (Kinsey 1985). Light curves of O₂ evolution by fragments of *T. ciliatum* blades at different temperatures (from 10   to 40  C) were measured in the laboratory by an open platinum electrode (Leletkin 1978). A halogen lamp with a capacity of 1 kW was used as a light source. Photosynthetically active radiation was isolated by glass light filters. Required illumination was established with the help of neutral glass light filters. In order to evaluate illumination, produced by the halogen lamp in the PAR region in a quantum flux density, the ratio $1 \text{ W} \cdot \text{m}^{-2} = 5 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ was used (McCree 1972).

The rate of oxygen evolution was measured as the difference between electrode records in the light and in the dark. The gross photosynthetic rate at saturation intensity of natural light was determined in those (and neighboring) blades in which the net photosynthesis (P_{net}) and dark respiration (R) had been measured by the Winkler method (Propp et al. 1982, Littler and Arnold 1985). Gross photosynthesis was then calculated at any point of a light curve by the formula:

$$P_i = \frac{P_{\text{max}} A_i}{A_{\text{max}}}$$

where P_i is the gross photosynthetic rate, in ml O₂·g dry wt⁻¹·h⁻¹; P_{max} is the gross photosynthesis rate at saturating light intensity determined by the Winkler method ($P_{\text{net}} + R$), in ml O₂·g dry wt⁻¹·h⁻¹; A_i is the gross photosynthetic rate, in μA of current; and A_{max} is the gross photosynthesis rate at saturating light intensity, in μA of current.

The radioactive method of measurement of light dependence of carbon assimilation is described in Chapter 9 of the present collection (Titlyanov et al. 1992). The radiocarbon method was used to measure the rate of net photosynthesis of macrophytes at different light intensities (Kolmakov and Tarankova 1978, Jensen et al. 1985).

RESULTS

Light curves of net photosynthesis (P_s vs. I) of the 2nd and 5th blades of *Thalassodendron ciliatum* from different depths measured at various water temperatures are presented at Figures 1 and 2. The shape of the curves is characterized by the following parameters: light intensity

corresponding to compensating point of photosynthesis (I_c), half-saturation ($I_{1/2}$) and saturation of photosynthesis (I_k), tangent of inclination of depths the initial section of the light curve ($tg\alpha$), maximal rates of net photosynthesis (P_{net}/max) and dark respiration (R). *T. ciliatum* is characterized by low levels of I_k ($30-50 \mu E \cdot m^{-2} \cdot s^{-1}$). And accordingly $0.5 P_{max}$ level is also reached at relatively low densities of incident flow ($I_{1/2}$ is from 5 to $25 \mu E \cdot m^{-2} \cdot s^{-1}$, whereas compensation of respiration (I_c) requires less than $5 \mu E \cdot m^{-2} \cdot s^{-1}$ of illumination. The steepness of the initial section ($tg\alpha$) of the photosynthetic light curve is from 30 to $65 \mu l O_2 \cdot g^{-1} \text{ fresh wt} \cdot h^{-1} \mu E^{-1} \cdot m^{-2} \cdot s^{-1}$ at *in situ* temperatures. Differences between young and old blades are displayed by an increase of the I_k level in the 5th blade for plants dwelling deeper than 1 m (Figs. 1 and 2). In old blades, the steepness of the initial section of a light curve ($tg\alpha$) also decreases. Light intensity which corresponds to the compensation point does not depend upon blade age.

The shape of the light vs. photosynthesis curves depends upon water temperature. In the majority of the experiments, photosynthetic rates on both the plateau region (P_{max}) and the linear section of the light curve (α) increase with the rise of water temperature from 10 to $30^\circ C$. Further increases in water temperature up to $40^\circ C$ lead to a decrease of both these values. In plants collected from 15 to 33 m and incubated in $40^\circ C$ water, photosynthesis was not saturated (I_k) even at $200 \mu E \cdot m^{-2} \cdot s^{-1}$. Extremely low temperatures ($10^\circ C$) caused irregular responses of the parameters I_k and I_c .

Maximal net photosynthesis and respiration at the natural temperature of a plant habitat ($27-28^\circ C$) are shown in Table 1. Both in young and old blades, net photosynthesis gradually increases while moving from the surface to 15 m in depth (1.5 and 1.8 times in the 2nd and 5th blades, respectively) and continuously decreases at further submergence down to 33 m (on the average by a factor of 1.4). The P_{net}/max level of young blades was at all depths 1.5 times higher than in old ones and at 33 m - 1.2 times higher. The respiration rates of the blades decrease with depth. The 5th blade has lower R values at all depths in comparison with the 2nd one (1.8 times at the surface and only 1.5 times at 33 m). The ratio of net photosynthesis to respiration is typical for marine macroflora: $2-4$ (Burris 1977, Titlyanov 1983). This parameter nearly doubles during the first 2 m in depth and then does not change substantially.

Plants from 15 m in depth showed the greatest potential photosynthetic activity, but it is unknown if higher capacities of deep water plants are realized *in situ*.

Values of daily net production calculated at different depths, depending on water clarity, are presented in Figure 3. Production is calculated for a day with average PAR values ($10-20 \mu E \cdot m^{-2} \cdot s^{-1}$ in the afternoon) in the period from $15-30$ January 1989, near Coetivy and Farquhar Islands. Photon flux density at various depths was calculated proceeding from spectral curves of penetration of a 1 m deep layer of different clearness (I-III ocean and 3 coastal types of water, Jerlov 1976). Waters of type I do not occur in the region of the Seychelles, they are taken as a case of maximal possible photosynthetic activity of plants at great depths. To evaluate the intensity of O_2 evolution, the ratio $mg O_2 = 0.3 mg C$ was used (McRoy and McMillan 1977).

Net production of *Thalassodendron ciliatum* blades changes with depth in the following way (Fig. 3). In the intertidal zone, young and old blades can accumulate 1.35 and $0.82 mg \cdot C \cdot g^{-1}$ fresh wt, respectively during 24 h. At $1-2$ m in depth, the carbon assimilation capacity increases in young blades 2.3 times, in old blades - 2.1 times (Table 1). At the first several meters of depth, daily net production exactly follows the increase of P_{net}/max , which indicates that plants dwelling there reach their peak photosynthetic capacities. At 15 m in depth, in the clearest waters (type I ocean) production of a young blade is essentially the same as at 2 m ($3.3 mg \cdot C \cdot g^{-1}$ fresh wt $\cdot 24 h^{-1}$), but old blade production increases up to $2.5 mg \cdot C \cdot g^{-1}$ fresh wt $\cdot 24 h^{-1}$. At 33 m in depth, production of both young and old blades drops to 2.3 and $1.9 mg \cdot C \cdot g^{-1}$ fresh wt $\cdot 24 h^{-1}$, respectively, in accordance with

P_{net}/max changes (Table 1). Thus, in the clearest waters, maximal photosynthetic capacities of *T. ciliatum* blades are reached at all depths and maximal production takes place at about 15 m. Even at 33 m in depth, the 24 h carbon balance is positive.

However, waters in the natural habitat show clarity values only between II ocean and 3 coastal types depending on meteorological conditions (Novozhilov et al. 1989). This means that a 10-fold drop of incident surface PAR occurs not at 100 m (as in the type I waters) but at 30, 15 and 8 m depths for waters of II, III ocean and 3 coastal types, respectively (Jerlov 1976). At depths of more than 2 m, production also changes depending on water type. In type II ocean waters, *Thalassodendron ciliatum* production at 15 m is lower than at shallower depths (Fig. 3). At 33 m in depth, production of the 2nd and 5th blades is approximately the same. In the most turbid waters of the 3 coastal type, production of young and old blades from 15 m in depth is only 33% and 50% of the maximum possible, and beginning from 26 m the carbon balance becomes negative. Thus, at 15 m in depth under natural conditions of illumination, the photosynthetic capacities of 1 g of young blade reaches 30-80% of the calculated maximal productivity, and 1 g of an old one - 20-70%. At 33 m in depth, these values for the 2nd and 5th blades range, respectively, from 0 to 80% and from 0 to 85%. The optimal depth for maximal primary production is about 2 m, where photosynthetic capacities of plants are actually reached. Positive 24 h balance of carbon determines the lower limit of *T. ciliatum* growth at 25-40 m which conforms to the ecological data obtained during our expedition (Ch. 5, Gutnik et al. 1992).

Temperature dependence of oxygen exchange in seagrass blades. Temperature is an important environmental factor affecting primary production of marine plants in tropical waters. On the islands studied, intertidal pools can be warmed up to 40°C and even higher during a day, and during rains they can be cooled to 20°C. On the other hand, deep water plants can be periodically cooled (to 20-15°C) due to up-welling (Novozhilov et al. 1989).

The temperature dependence of net photosynthesis for *Thalassodendron ciliatum* blades from various depths (Figs. 4 and 5) shows a maximum between 25-32°C and is not dependent on blade age or depth. Variations in the maximum levels were mainly correlated with the light intensity at which the temperature dependence was registered. For example, in plants from 15 m in depth exposed to low light (α section of the light curve), the maximal rate of O_2 evolution occurred at 28°C for young blades and at 25°C for old blades, whereas at light saturation, 32°C was required to reach the maximum. The greatest differences between plants were correlated with their sensitivity to temperature changes, which can be characterized by the coefficient $Q_{10}^{-\Delta P/\Delta T \cdot P_{max}}$, where ΔP = the change of net photosynthesis rate in the interval $\Delta T = 10^\circ C$; P_{max} = net photosynthetic rate in the maximum of the temperature curve. Values of this parameter for O_2 evolution rate at light saturation with reference to blade age and habitat depth are given in Table 2. A 10° C drop in temperature from optimal causes a similar decrease in the photosynthesis rate in both young and old blades, which is more pronounced (up to 60%) in plants from 2 and 33 m depths and minimal in plants from the surface (37%). A 10° temperature increase above optimal also causes a decrease of net photosynthesis, but differs between the 2nd and 5th blades and is minimal for shallow water plants. Variations of Q_{10} are interesting since they suggest a greater resistance of photosynthesis to temperature fluctuations in plants from the intertidal zone where such fluctuations are the most frequent.

The dark respiration rate increases up to 40°C, with growth in all the samples except plants from 2 m in depth (Figs. 4 and 5). Respiration of these plants is maximum at temperatures corresponding to the photosynthetic optimum. At the extremes of the temperature intervals, rates of O_2 uptake differ as much as 4-6 times.

Light dependence of carbon assimilation in seagrass blades (P_s vs. I). The carbon

photoassimilation rate was studied with reference to light intensity in *Thalassodendron ciliatum* from various depths during different times of the day in order to determine the daily dynamics of photosynthesis in middle aged blades (3rd and 4th, Fig. 6). For these experiments, plants from various depths were put in aquaria shaded by white cloth to establish illumination conditions close to those in the natural habitats. During 1-3 days of adaptation, the light dependence of photosynthesis was determined during the morning, afternoon and evening hours.

Daily fluctuations in the carbon photoassimilation rate were approximately the same in plants from different depths. The photosynthetic rate at saturating light intensity (P_{\max}) increased during the first half of the day and dropped during the afternoon. The maximal rate (P_{\max}) was observed at 1300 in blades from 0-26 m in depth, with 7 to 8.5 mg CO₂·g dry wt⁻¹·h⁻¹. P_{\max} in plants from 33 m in depth was only half this value.

In plants from 0, 2-3 and 5 m depths, the initial slope of the light curve (α) decreased from morning to evening hours, i.e., the efficiency of utilization of low light declined. Clear day changes of this parameter were not recorded for plants from 11, 26 and 33 m depths. A light curve plateau was not found in all the experiments (1300 h, 2-3 m depth; 0800 h, 11 m depth). There were no clear patterns in the daily fluctuations of the light level at which photosynthetic light saturation (I_k) occurred. In the majority of cases, light saturation of CO₂ assimilation occurred at relatively low PAR intensities: between 50 and 100 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Photosynthetic inhibition by light fluxes of more than 240 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ took place during morning hours in plants from 0, 5 and 33 m, in the afternoon - from 5 and 33 m and in the evening - from 0.5, 2-3, 11, 26 and 33 m. The middle-aged blades displayed daily variations in the carbon assimilation rate (P_{\max}), as did young (2nd) and old (5th) blades of plants taken from both intertidal pools (0.5 m depth) and from the subtidal zone (2 m in depth).

The amplitude of daily fluctuations of P_{\max} was greater in intertidal plants than in plants from 2 m in depth. The greatest difference of P_{\max} between the afternoon and evening hours (4.5 mg CO₂·g dry wt⁻¹·h⁻¹) was recorded in old blades of *Thalassodendron ciliatum* inhabiting intertidal pools.

On the basis of the light curves presented at Figure 6 and additional measurements, the potential net production per day for plants taken from all depths (0 to 33 m) was calculated (Fig. 7). Primary net production was calculated by the method of graphic summation (Nichiporovich 1956), i.e., potential photosynthetic production P_{\max} for each daylight hour (from 0800 to 1700 h) was summarized. The maximum potential net production occurs in plants from the middle depths (from 6 to 23 m), and the minimum one - to intertidal and deep water (33 m) plants.

DISCUSSION

The light curves of net photosynthesis of *Thalassodendron ciliatum* blades are close in general shape to those of other seagrass species (Buesa 1974, Dennison 1985). However, *T. ciliatum* shows very early saturation of photosynthesis ($I_k = 30\text{-}50 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in comparison with *Zostera marina* (65-120 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Dennison and Alberte 1985) or *Thalassia testudinum* (about 170 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, Buesa 1974, King and Schramm 1976).

The rates of $P_{\text{net}}/\text{max}$ and R rates are close to those of other species of seagrasses (Jones 1968, Buesa 1974, Heffernan and Gibson 1983). Fluctuations of these parameters for *Thalassodendron ciliatum* are similar to those reported earlier for macrophytes (Ramus et al. 1976, 1977).

Light curves of carbon assimilation differ from those of oxygen evolution mostly due to the I_k index which is shifted towards greater light intensities in the light curves of carbon assimilation. This

shift can be explained by difference in the method of light curve determination. Changes of functional indices of light curves of O_2 evolution and CO_2 uptake connected with habitat depth are close to each other. These are stable and show a high level of P_{max} for plants from middle depths (2-15 m for O_2 evolution and 6-23 m for CO_2 uptake) and also a drop in P_{max} for intertidal and deep water plants. There are tendencies in the increase of the slope of the linear section of both light curves (O_2 and CO_2) and adaptation to the decrease of light quantity with depth (from 0 to 26 m).

On the basis of the data, the depth distribution of *Thalassodendron ciliatum* primary production of blades is determined by light conditions which also limit the lower boundary of the species distribution. On the islands studied, maximal seagrass productivity was found at about 2 m in depth which is not exposed to air at low tide. Relatively high photosynthetic production at middle and lower depths is maintained due to physiological adaptation to light. This phenomenon is rather well studied in terrestrial plants and marine algae and is characterized specifically by the increase of photosynthetic capacities and the decrease of respiration with depth (Titlyanov 1983, Titlyanov et al. 1987).

Temperature curves of net photosynthesis of *Thalassodendron ciliatum* have the classical shape with well-expressed temperature optimum at 28-30°C. Measured temperature optimum of *T. ciliatum* photosynthesis is close to the temperature optimum of growth of tropical seagrass *Thalassia testudinum* from Biscayne Bay, Florida (near 30°C at salinity 30ppt., Zieman 1975).

The position of the temperature optimum is less dependent on depth which was shown for macroalgae (Kanwisher 1966, Yokohama 1972, Katayama et al. 1985).

The study of temperature effects on the primary production of *Thalassodendron ciliatum* revealed that a 10° temperature rise from optimal (28-30°C) for Δt interval during daylight hours at shallow depths leads to a drop of net production equal to $Q_{10} \cdot P_{net}/max \cdot \Delta t$, where P_{net}/max - net photosynthesis rate at the temperature optimum. In comparison with 24 h production, which on the shallows is determined by the product $P_{net}/max \cdot L$, where L - day length, the loss makes $Q_{10} \cdot \Delta t \cdot L^{-1}$ percent. Thus, if temperature increases during the entire day, the loss of 24 h production is equal to Q_{10} percent, which does not exceed 30% for shallow plants. Similar considerations can be applied in the case of a temperature drop at shallow depths, where the loss of photosynthetic production can reach 60% at 20°C (Table 2).

As was shown for three species of seagrasses from Florida - *Thalassia testudinum*, *Syringodium filiforme* and *Halodule wrightii* (McMillan 1984) - tropical seagrass species have high heat tolerance and can survive temperatures of 36°C for 4 weeks and 39°C for up to 36 h.

Nighttime drops in temperature and the attendant decrease in respiration leads to an increase in the 24 h net production. To estimate the effects of R decreases the 24 h carbon balance, the following ratio was used: $P_{net} \cdot 24h^{-1} = P_{net}/day - R_{night}$, where $P_{net}/24h$ and P_{net}/day - 24 h and daily net production, R_{night} - total night respiration. If the respiration rate during the night is K times less, then taking into account that $P_{net}/max / R = N$ (Table 1) and using the equation of balance, it is easy to show that the 24 h production increases $(N - 1/k)/(N-1)$ times. For shallow algae, for example, a nighttime water temperature of 20°C can cause an increase in 24 h production by 1.5 fold in comparison with the optimal temperature (28-30°C).

It is interesting to note that production increases due to a drop in the respiration level can be reached also by a change of salinity. Thus, for the seagrass *Ruppia maritima* from Tampa Bay, Florida (Dawes 1974), a salinity rise at the same illumination level leads to a drop in the dark respiration without change of photosynthesis.

Changes of potential photosynthetic capacities (CO_2 assimilation) within a day for the seagrass *Thalassodendron ciliatum* are the same as for temperate and tropical macroalgae (Titlyanov et al. 1991). They are expressed in the increase of P_{max} rate towards the afternoon and in its drop toward evening. This feature was found in blades of all ages. The decrease in slope of the linear section of the light curve of CO_2 assimilation from morning to evening hours is probably connected with the drop of chlorophyll concentration in *T. ciliatum* blades, as was shown for *Ulva fenestrata* thalli (Titlyanov et al. 1978).

High stable levels of potential photosynthetic capacities of *Thalassodendron ciliatum* blades which are maintained down to 23-26 m in depth is very important for the distribution of this seagrass into great depths. As revealed by our calculations, high potential photosynthetic capacities can be realized with high efficiency over a wide illumination range which leads to a stable high productivity throughout the depth range from 2 to 33 m, both in clear and turbid waters of the Seychelles (Fig. 3).

Stable levels of primary production of benthic autotrophs over a wide range of illumination was reported earlier for reef-building corals (Titlyanov et al. 1988) and for tropical macroalgae (Titlyanov et al. 1992, Ch. 9, this volume).

High production over a wide illumination range is a result of adaptation of benthic macrophytes to the natural habitat illumination. This is attained via a number of adaptive reactions which are not the same for different groups of aquatic plants (Titlyanov et al. 1987). For *Thalassodendron ciliatum*, adaptation to low light intensities in deeper waters leads to lower light saturation of photosynthesis, accumulation of photosynthetic pigments, an increase in the slope of the linear section of the light curve and a greater photosynthetic level at light saturation (Titlyanov et al. 1992, Ch. 9, this volume).

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Table 1. Rates of net photosynthesis at light saturation (P net/max) and dark respiration (R) at 27-28°C for young and old blades of *Thalassodendron ciliatum* from different depths. "*" maximal deviation from average value at n=4.

Depth m	Blade net/max No.	$\mu\text{l O}_2\cdot\text{g fresh wt}^{-1}\cdot\text{h}^{-1}$		P
		P net/max	R	R
0	2	0.671±0.146	0.335±0.055	2.0±0.9
	5	0.411±0.016	0.191±0.015	2.1±0.3
2	2	0.895±0.044	0.193±0.032	4.6±1.2
	5	0.569±0.1	0.147±0.051	3.9±3.0
15	2	0.983±0.024	0.250±0.05	3.9±1.1
	5	0.753±0.022	0.178±0.046	4.2±1.6
33	2	0.680±0.02	0.175±0.005	3.9±0.2
	5	0.580±0.02	0.160±0.02	3.6±0.6

Table 2. Values of Q_{10} coefficient for the 2nd and 5th blades of *Thalassodendron ciliatum* from different depths at temperatures lower and higher than 30°C.

Depth, m		Q_{10} at Temp. 20-30°C		Q_{10} at Temp. 30-40°C
0	37	33	-20	-12
2	62	58	-30	-14
15	45	47	-23	-36
33	60	50	-20	-20
Blade No.		2	5	2
				5

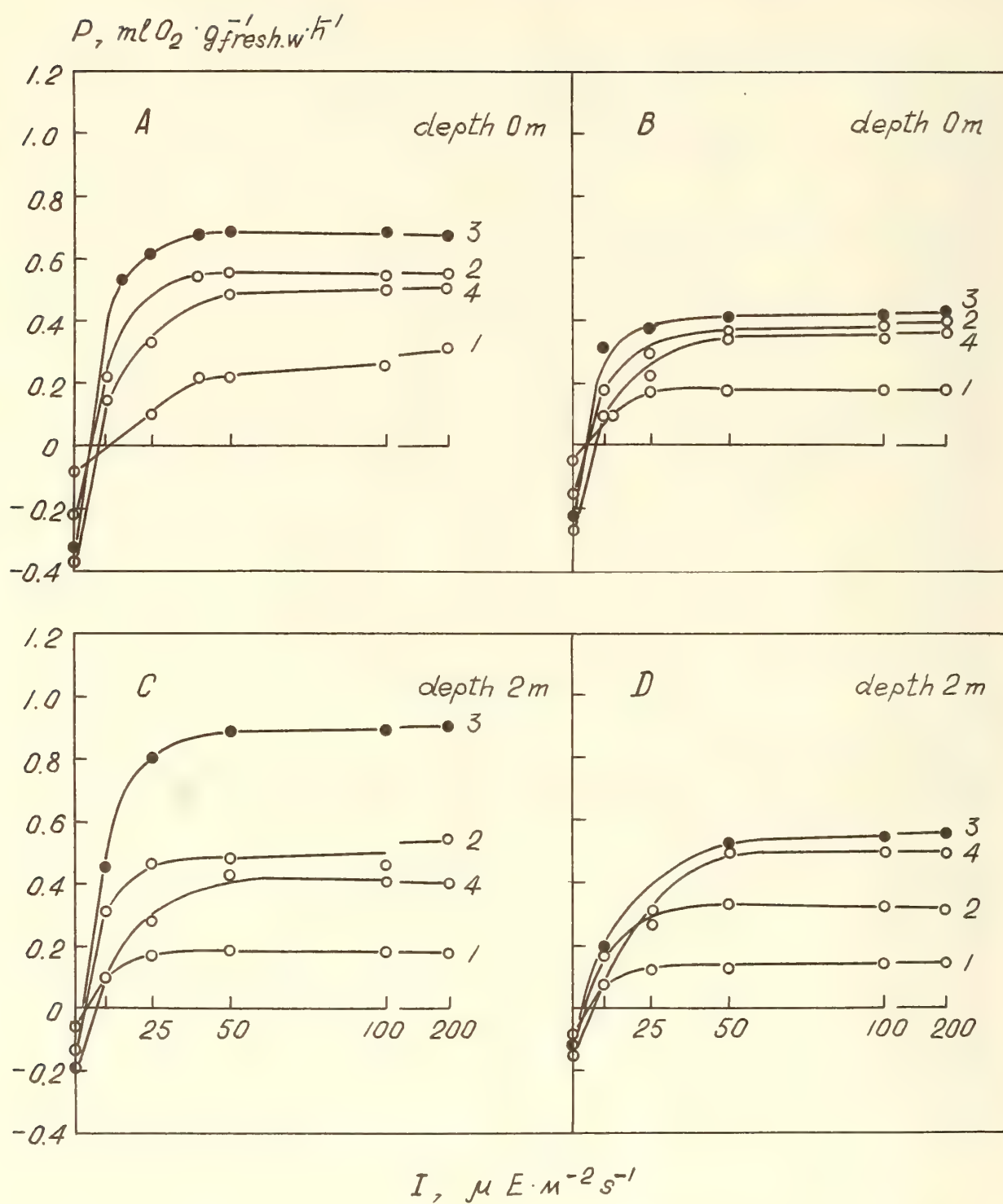


Figure 1. Light curves of photosynthesis of the 2nd (A,C) and 5th (B,D) leaves of *Thalassodendron ciliatum* from 0 and 2 m in depth at different temperatures (1=10°, 2=25°, 3=30°, 4=40°C).

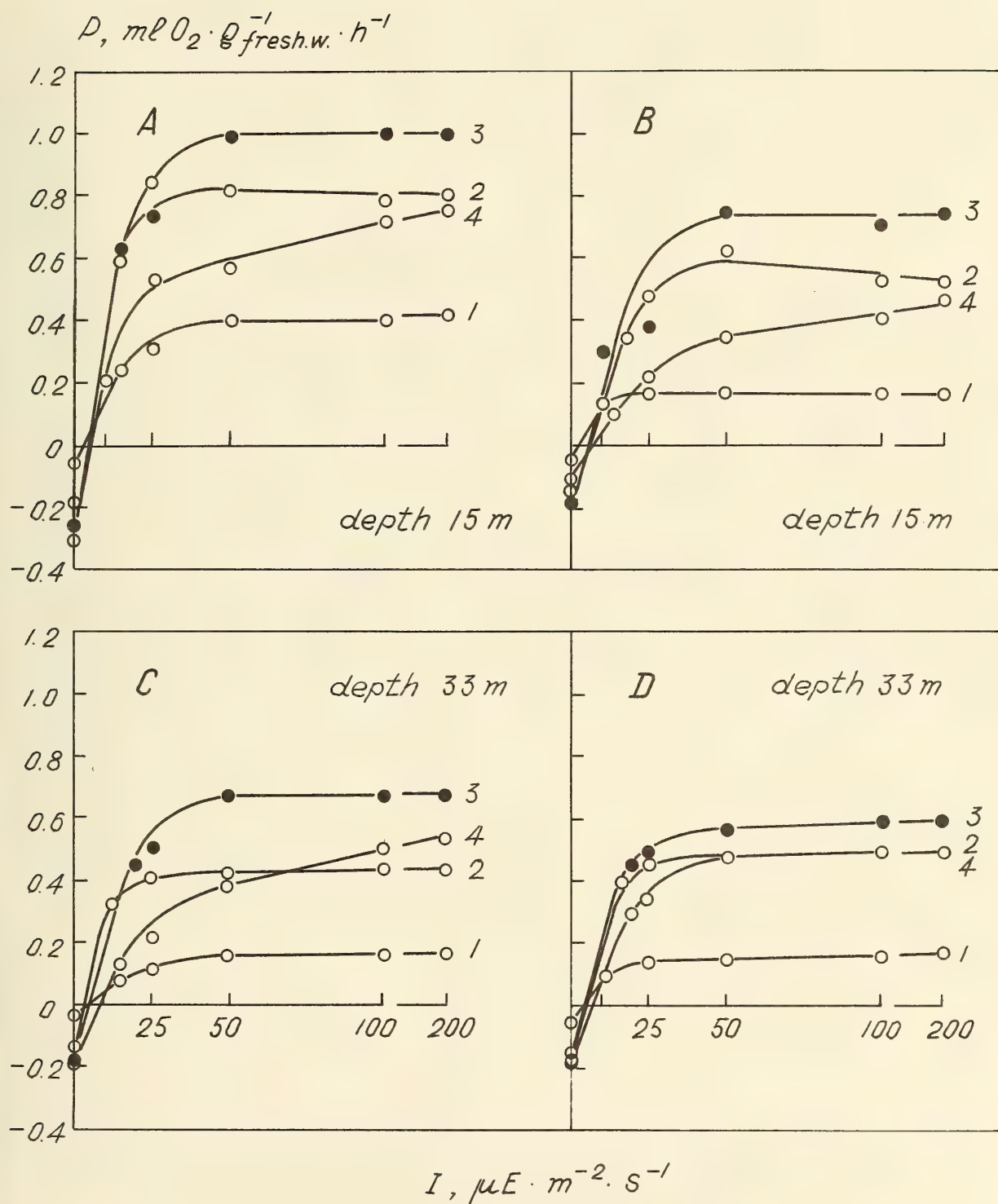


Figure 2. Light curves of photosynthesis of the 2nd (A,C) and 5th (B,D) leaves of *Thalassodendron ciliatum* from 15 and 33 m in depth at different temperatures (1=10°, 2=25°, 3=30°, 4=40°C).

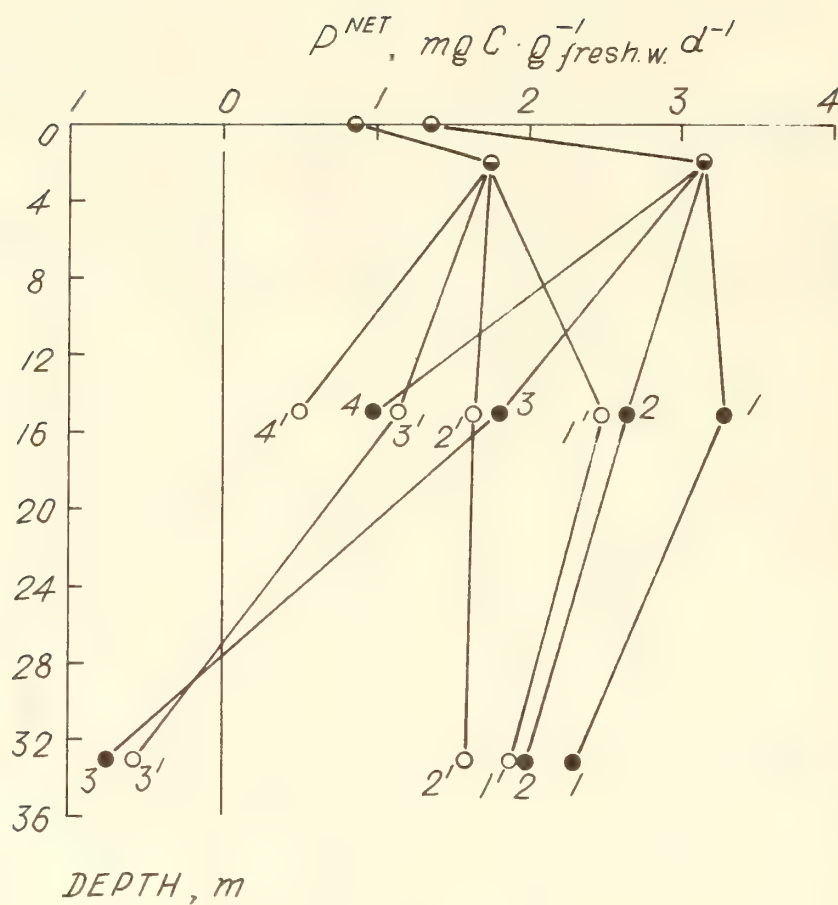


Figure 3. Daily net photosynthetic production (P^{net}) as a function of depth in the 2nd (1-4) and 5th (1'-4') leaves of *Thalassodendron ciliatum* in waters of different transparency: 1 - Type I, 2 - Type II and 3 - Type III oceanic waters, 4 - Type III coastal waters (Jerlov 1980).

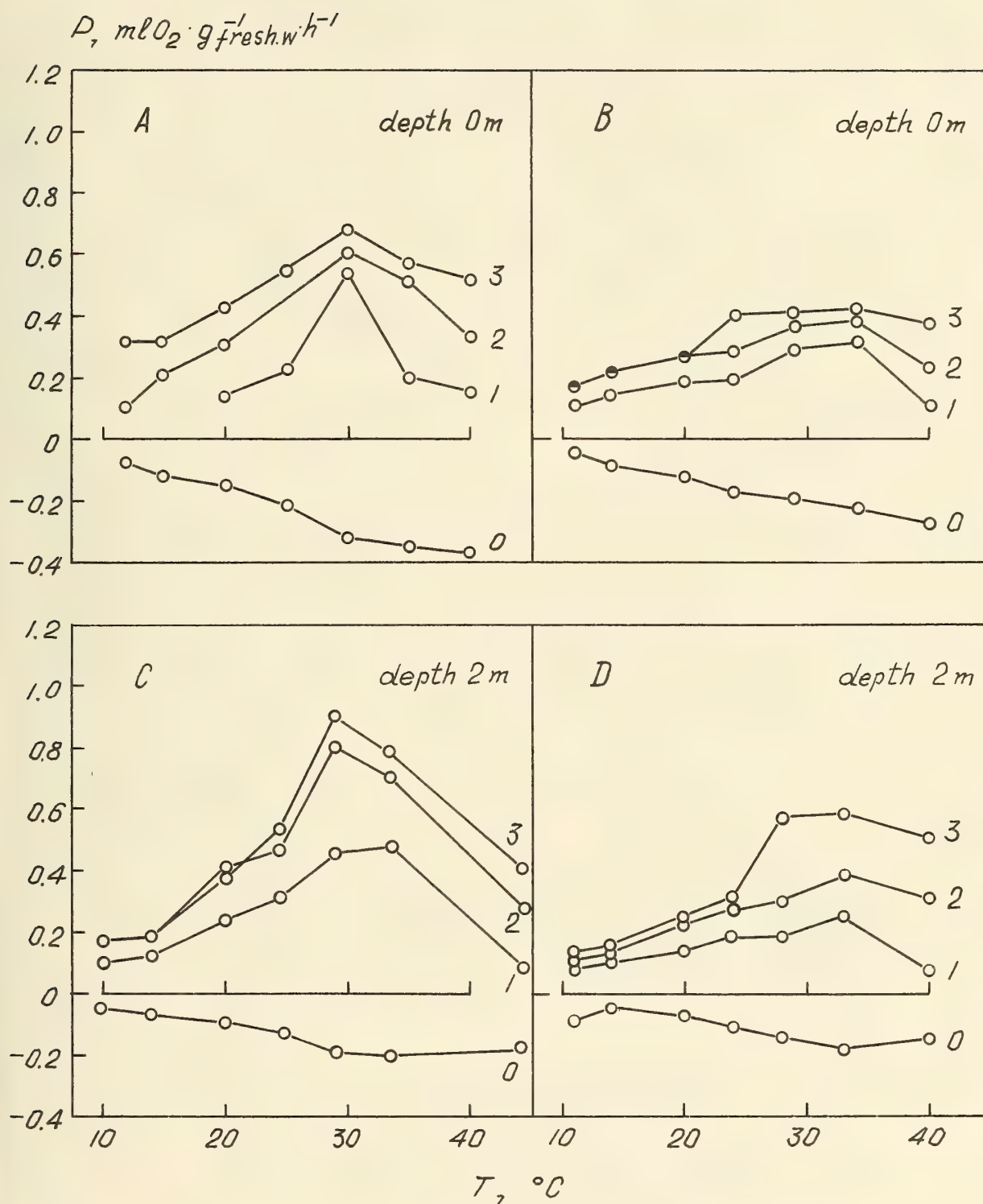


Figure 4. Temperature dependence of photosynthesis and dark respiration in the 2nd (A,C) and 5th (B,D) leaves of *Thalassodendron ciliatum* from 0 (A,B) and 2 (C,D) m in depth at different intensities of photosynthetic flow density: 0 - dark respiration; 1, 2, 3 for 10, 25 and 200 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, correspondingly.

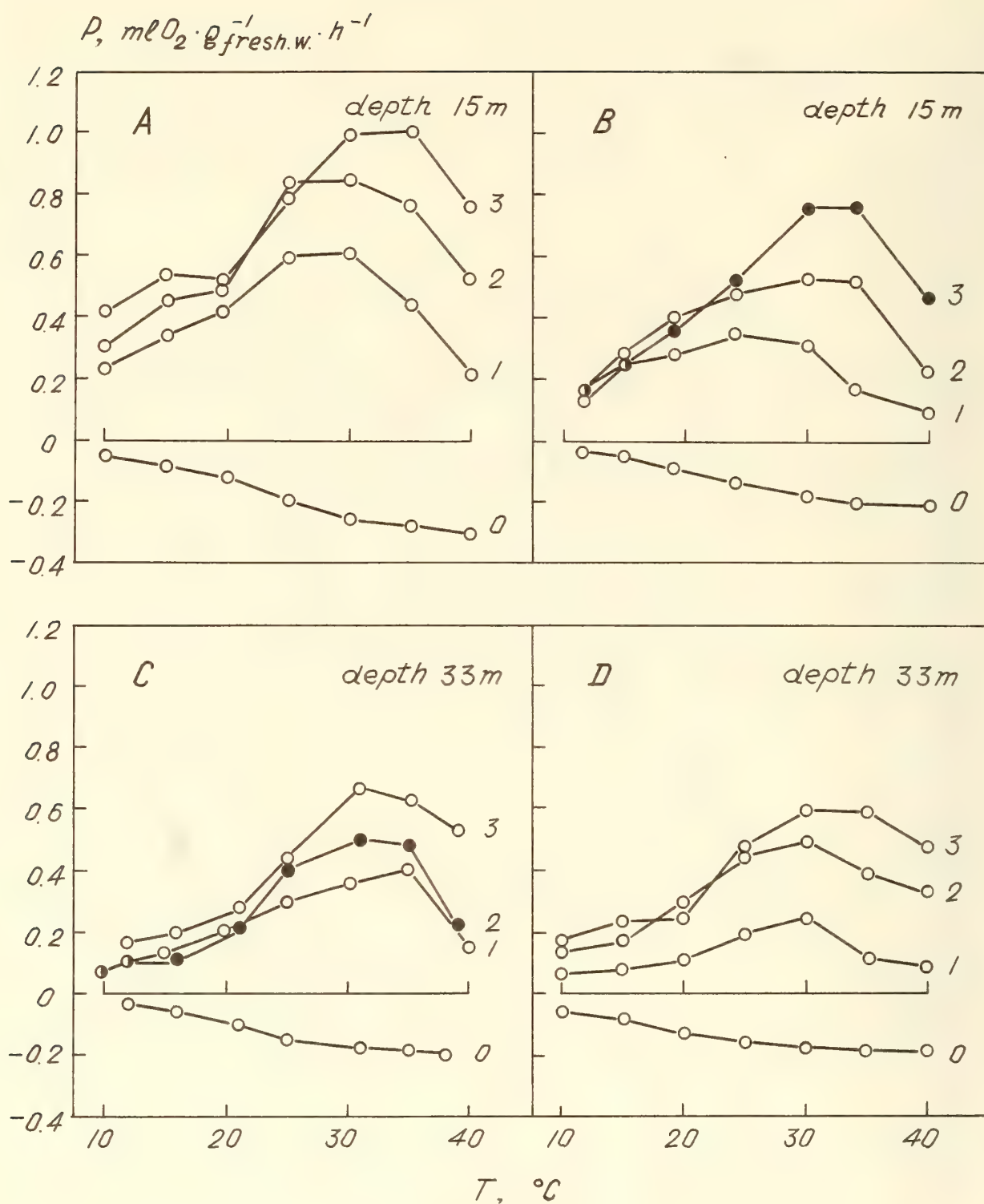


Figure 5. Temperature dependence of photosynthesis and dark respiration in the 2nd (A,B) and 5th (C,D) leaves of *Thalassodendron ciliatum* from 15 (A,B) and 33 (C,D) m in depth at different intensities of photosynthetic flow density: 0 - dark respiration, 1, 2, 3 for 10, 25, and 200 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, correspondingly.

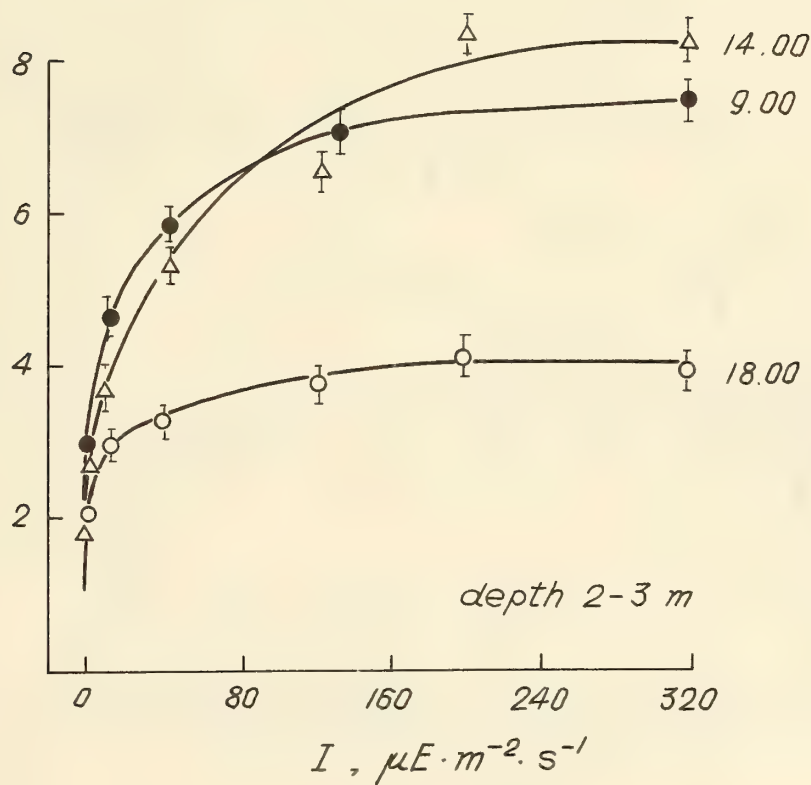
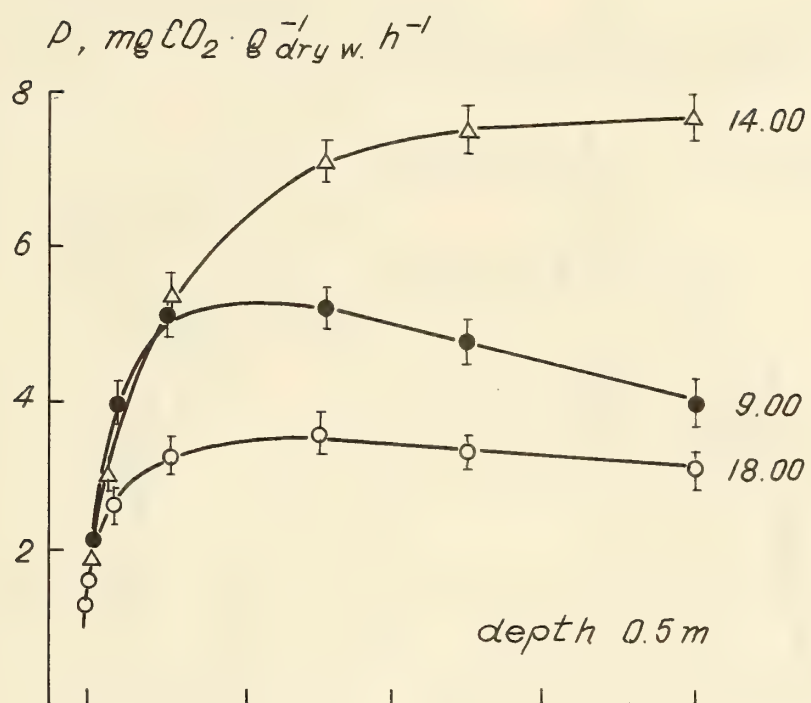


Figure 6 (A). Light dependence of photosynthesis in *Thalassodendron ciliatum* at various times of the day for a given depth.

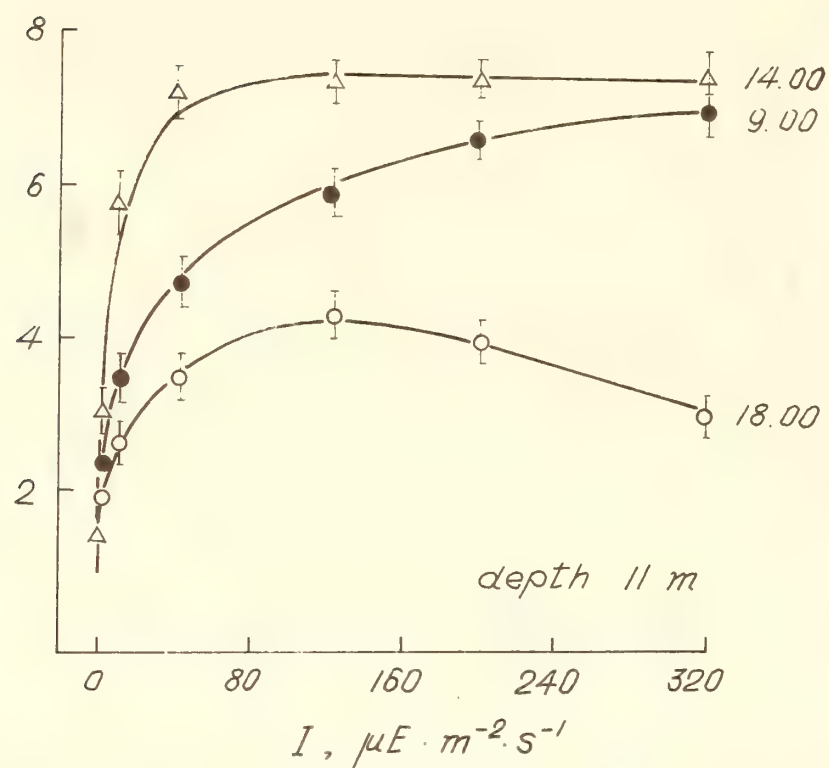
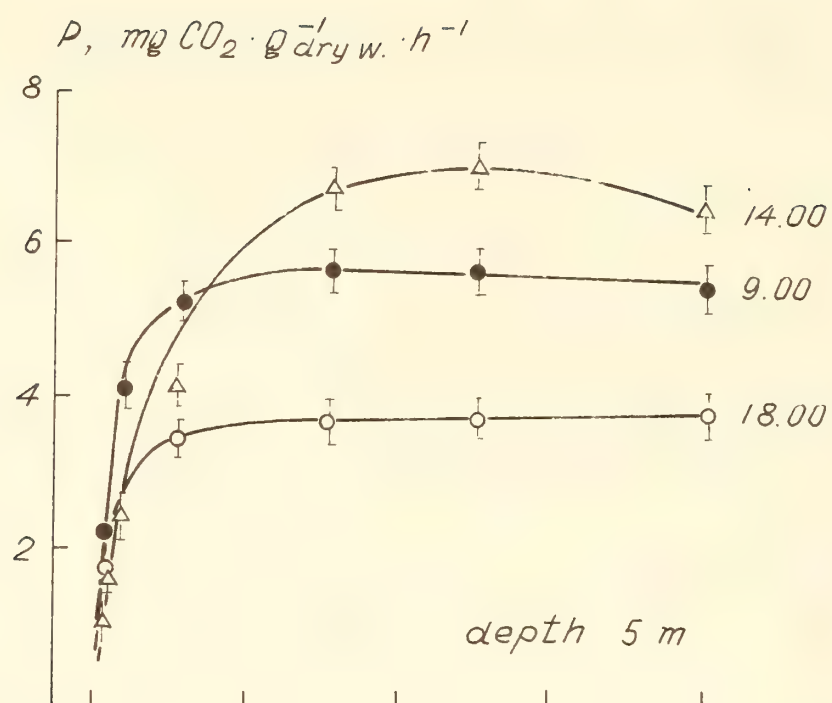


Figure 6 (B).

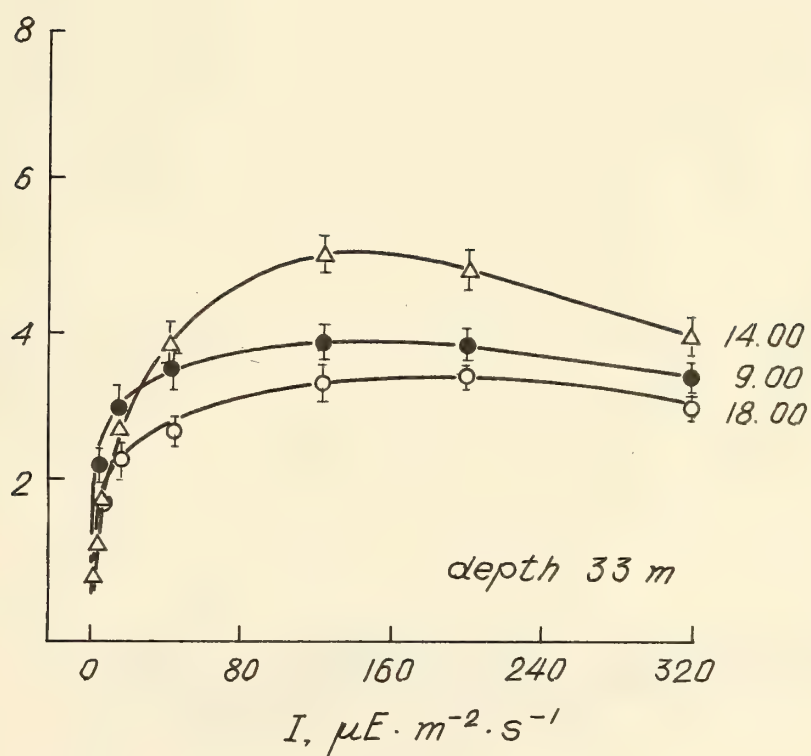
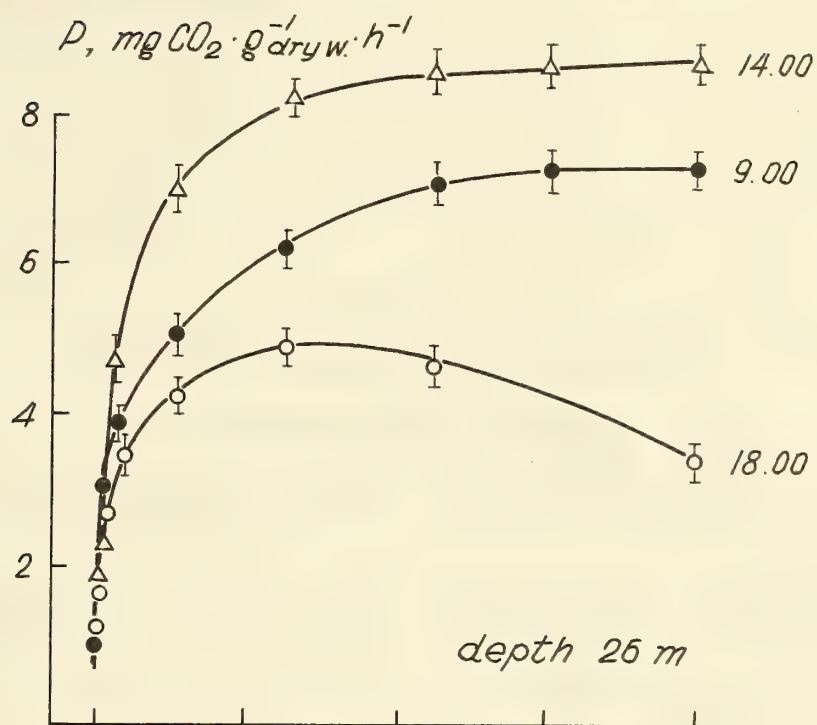


Figure 6 (C).

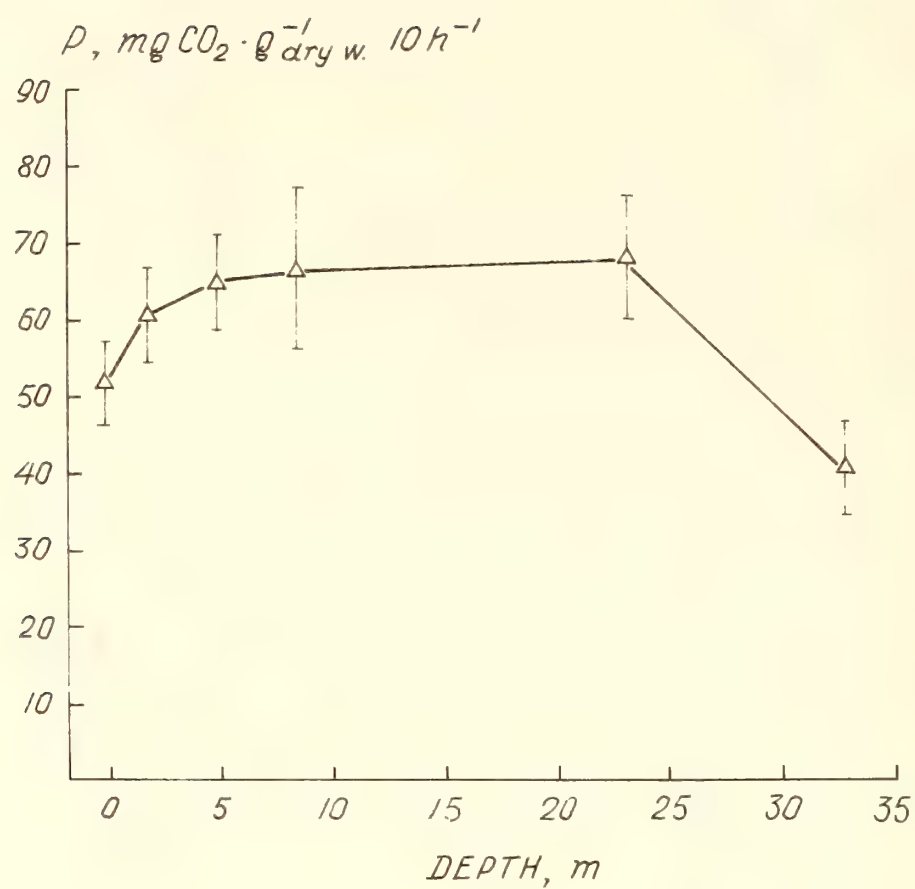


Figure 7. Daily potential production of middle-aged leaves of *Thalassodendron ciliatum* with reference to habitat depth.

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CHAPTER 12

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THALASSODENDRON CILIATUM:

LEAF MORPHOLOGY AND CARBON METABOLISM

BY

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T.R. Pärnik^{*}, K.Y. Bil^{**}, P.V. Kolmakov^{***} and E.A. Titlyanov^{***}

ABSTRACT

The kinetics of the incorporation of ^{14}C into photosynthates during labeling and pulse-chase experiments has shown that the seagrass *Thalassodendron ciliatum* (Forskål) den Hartog is a typical C_3 plant. Both adaxial and abaxial leaf surfaces lack stomata and are covered with a thin layer of epidermal cells containing chlorophyll. 80% of the leaf volume is occupied by chlorophyll-free heterotrophic cells. Respiration of these unpigmented cells is equivalent to 66% of the gross photosynthetic rate. The molar rate determined from $^{14}\text{CO}_2$ fixation during a 10 min exposure is 0.2 m mol CO_2 per g dry weight per hour and exceeds the apparent O_2 release by 3 fold. Environmental conditions favorable for *Thalassodendron ciliatum* extend to the depth of 26 m. The half-maximum $^{14}\text{CO}_2$ uptake rate is achieved at a light level of $1.5 \text{ W}\cdot\text{m}^{-2}$ in plants from both deep (33 m) and shallow (0.5 m) waters. In plants growing 33 m deep, photoassimilation of CO_2 is relatively slow at all light intensities and tissues contain higher levels of flavonoids. The amino acid contents of mature leaves are identical in shallow and deepwater plants, whereas the younger leaves of deepwater plants are poorer in proline and cystein. In contrast to terrestrial plants, the pH in the sap of heterotrophic cells increases during the daytime and reaches a value of 6.1 by nightfall. Acidification of the sap reaches pH 5.6 from dawn into early morning due to the formation of malate from bicarbonate in the dark.

INTRODUCTION

The seagrass *Thalassodendron ciliatum* (Forskål) den Hartog [formerly known as *Cymodocea ciliata* (Hartog 1970)] is an inhabitant of the Red Sea, western areas of the Indian Ocean, coasts of Egypt, Sudan, Iran, Saudi Arabia, Somalia, Kenya, Tanzania, Mozambique, South Africa, Madagascar, Chagos Archipelago, Seychelles Islands and Comoro Islands. *Thalassodendron ciliatum* has also been found in waters of Indonesia, New Guinea, Philippines, Solomon Islands, Caroline Islands, China and the northwest to northeast coasts of Australia (Hartog 1970, 1990, Meñez et al. 1983, Walker and Prince 1987). *Thalassodendron ciliatum* occupies the upper sublittoral zone to the depth of 40 m and forms mats up to 30-40 cm in thickness. It normally grows at temperatures from 26 to 30°C, but in littoral basins it withstands temperatures up to 38°C. The average biomass of T.

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ciliatum reaches 6050 g fresh wt·m⁻² (Aleem 1984).

Detailed descriptions of *Thalassodendron ciliatum* as well as information concerning its environmental requirements are available in the literature (Hartog 1970, Mefez et al. 1983, Aleem 1984, Johnstone 1984, Walker and Prince 1987). However, its physiology and biochemistry are poorly studied. This paper provides new data on the morphology of the leaf of *T. ciliatum* as well as the biochemistry of its photosynthetic carbon metabolism, which was investigated during an expedition to the southwest Indian Ocean from January to March 1989 on the R/V Akademik Aleksander Nesmeyanov.

MATERIALS AND METHODS

Thalassodendron ciliatum was sampled near the islands of C  etivy, Farquhar, Aldabra and Desroche from shallow waters down to 33 m deep. The samples collected for experiments were kept in glass tanks flushed with running seawater. The plants used in biochemical studies were free of visible epiphytes.

Dependence of photosynthesis on light intensity was studied by the uptake of the radioactive carbon isotope, ¹⁴C. Each experimental set included three replicate leaves and exposures were carried out in a chamber that measured 25x25x3 cm. Leaves were illuminated with a DRL-700 fluorescent lamp that provided a maximum intensity of white light of 80 W·m⁻². To convert illumination produced by the fluorescent lamp in the PAR region to quantum flux density, use the ratio 1 W·m⁻² = 5μE·s⁻¹. Lower intensities were obtained by applying neutral density filters with transmission quotients of 0.2, 0.5, 1.4, 10.0, 14.0, 38.5 and 63%. Before exposure to ¹⁴CO₂, the leaves were flushed in the chamber for 20 min with seawater. Thereafter, NaH¹⁴CO₃ was added for 20 min and the radioactive solution was removed, leaves were washed with seawater, killed at 100°C and dried to constant weight at 40-60°C. The samples were then ground in a micromill and their radioactivity was measured by means of the Geiger-Mueller counter method of Bykov and Koshkin (1969).

The rate of net photosynthesis (P_N) and dark respiration (R_D) were measured by the rate of O₂ increase or depletion in a closed system, which consisted of a leaf chamber (17.5x7x1.1 cm), a membrane pump and an oxygen detector. The concentration of O₂ was measured by means of the general-purpose oxygen meter Nr.5221 with oxygen sensor Nr.5972 (Zaklady Elektroniczne "ELWRO", Wroclaw) and recorded by means of a TZ 4100 potentiometer (Laboratorni Pristroje, Prague). The volume of the system was 200 cm³ and the flow rate of seawater was 120 cm³·min⁻¹. The sensor was calibrated at two O₂ concentrations before each experiment. An O₂ concentration of zero was obtained by adding a few crystals of dithionite (N₂S₂O₄). The other O₂ concentration for calibration corresponded to air-saturated seawater at the temperature of the experiment.

Exposure of leaves for the investigation of photosynthates was carried out in standard 50 ml beakers. Portions of leaves were weighed and placed into seawater for a 20 min pre-illumination period and then transferred to seawater containing H¹⁴CO₃⁻. After the period of illumination, the leaves were rinsed with seawater and killed in boiling ethanol acidified with formic acid. In pulse-chase experiments, the leaves were incubated under the experimental period of illumination with H¹⁴CO₃⁻ and thereafter rinsed and transferred to non-radioactive seawater and killed.

The fixed leaf material was ground in a mortar and its radioactivity was measured by the Geiger-Mueller counter. Ethanol- and water-soluble photosynthates were separated by means of two-dimensional paper chromatography (Benson et al. 1950, V  rk et al. 1968, Bil' et al. 1981). The radioactivity of components was measured by means of a SL-30-300 scintillation counter

(Intertechnique, France) and a LS 100 C (Beckman, Austria). Amino acids were estimated by means of an AAA-339 amino acid analyzer (Mikrotechna, Czechoslovakia).

The pH of the sap of heterotrophic cells was measured over a 24 h period at 2.0 h intervals. Epidermal cells of the adaxial side of the leaf were removed by means of a razor blade and the pH of the cell sap was determined by means of Multiphan indicator paper (Chemapol, Czechoslovakia).

RESULTS AND DISCUSSION

Fig. 1 shows that both adaxial and abaxial surfaces of the leaf are covered with a thin layer of chlorophyll-containing epidermal cells that lack stomata. The leaf blade contains a number of parallel vascular bundles each surrounded by a layer of small unpigmented cells probably representing a mestome sheath. Vascular bundles occupy the middle part of the leaf blade and are connected to each other by means of cross veins. The vascular system is surrounded by large colorless vacuolized cells.

As can be seen from the photosynthesis vs. light curves (PI, Fig. 2), the previous conditions of illumination in the natural habitat have a strong influence upon the functioning of the photosynthetic apparatus. The diurnal kinetics of photosynthesis show that the maximum CO_2 uptake activity is observed at noon. The plateau region of the PI curves depends on the habitat, being reached at 20 to 30 $\text{W}\cdot\text{m}^{-2}$ in plants from deep waters and at 50 to 80 $\text{W}\cdot\text{m}^{-2}$ in plants from depths of 0.5 to 6 m. The initial slopes of the PI curves are also different (Fig. 2), with the half-maximum rate being reached at 1.5 $\text{W}\cdot\text{m}^{-2}$ and 5 $\text{W}\cdot\text{m}^{-2}$ in plants from deep and shallow waters, respectively. The greater sensitivity of the *T. ciliatum* photosynthetic apparatus in the range of lower light intensities facilitates efficient operation in natural low light habitats, analogous to macroalgae (Titlyanov et al. 1987). The increase in the photosynthetic capacity of *Thalassodendron ciliatum* as a function of depth to 26 m is distinct from other macrophytes and is difficult to explain. In plants from the deepest habitats, the slope of the PI curve is relatively small and at high light intensities assimilation of CO_2 is even inhibited. This is probably not a typical photoinhibitory reponse which occurs at high light intensities, because it takes place at very low light intensities of about 3 $\text{W}\cdot\text{m}^{-2}$. Rather, it appears to be a phenomenon of adaptation of these plants to unfavorable environmental conditions.

In order to get reliable values of radioactivity, the leaves of *Thalassodendron ciliatum* had to be exposed to $\text{H}^{14}\text{CO}_3^-$ for at least 20 min. During that time, a significant portion of the label is incorporated into intermediates of the glycolate pathway and into C_3 and C_4 acids. Since these products are decarboxylated, the calculated values of $^{14}\text{CO}_2$ influxes are less than the true rate of photosynthesis (P_T), but they exceed net photosynthesis (P_N) measured by $^{12}\text{CO}_2$. In the experiments with the isotope, the release of CO_2 at the expense of unlabeled end products of photosynthesis and from heterotrophic cells has not been taken into account.

Since heterotrophic cells make up to 80% of the volume of the leaf blade and photosynthetic cells only 20%, it is interesting to compare the $^{14}\text{CO}_2$ uptake and the concurrent O_2 release. The molar $^{14}\text{CO}_2$ uptake exceeded the apparent O_2 release by threefold (Table 1), apparently due to a very high respiration rate of the heterotrophic cells. Since the ratio of CO_2/O_2 during photosynthesis is unity, one may deduce that the respiration rate of the *Thalassodendron ciliatum* leaf is about 66% of the true photosynthetic rate and exceeds net photosynthesis by 1.5- to 2-fold. This agrees with the finding that the O_2 uptake rate immediately after switching off the light ("dark" respiration in the light) could be twice the rate of net photosynthesis. Therefore, application of the photosynthetic coefficient is not reasonable while the ratio of CO_2/O_2 is indefinite, due to the heterotrophic cells.

Mechanisms of photosynthetic carbon metabolism are not as well investigated in marine plants as in terrestrial plants. Their characteristics do not always allow a plant to be classified unequivocally as belonging to the C_3 or C_4 type. For example, *Thalassia hemprichii* (Ehrenb.) Aschers, growing in the same area of the ocean as *Thalassodendron ciliatum*, has a coefficient of isotope discrimination $^{13}C/^{12}C$ characteristic of the C_4 type of photosynthesis; however, studies of its $^{14}CO_2$ metabolism reveal that it is a C_3 plant (Andrews and Abel 1979). We applied two different approaches to study the photosynthetic metabolism of *T. ciliatum*: (1) kinetics of the incorporation of ^{14}C from $^{14}CO_2$ into photosynthates and (2) the pulse-chase method.

Kinetic curves (Fig. 3) show that the initial rate of ^{14}C uptake is higher than the rate following a 2 min exposure at both limiting and saturating light intensities (respectively, 2 and 1.2 fold). Such a kinetic is characteristic of C_3 photosynthesis, as observed with terrestrial photorespiring plants. After a 35 sec labeling period, 72% of the ^{14}C was found in sugar phosphates and 12% in malate and aspartate (Table 2), which is also characteristic of C_3 metabolism. However, at a very low light intensity ($0.15\text{ W}\cdot\text{m}^{-2}$, the products of the PEP carboxylation, malate and aspartate, contained 41% ^{14}C incorporated during the 35 sec exposure. At longer exposures, the rate of the synthesis of sugars decreased and the relative rate of the synthesis of alanine increased. This was probably a result of a decrease in the PGA reduction rate and its conversion into pyruvate and alanine as an alternative route of metabolism. The relative rate of PEP carboxylation was also increased and led to an enhancement of the efflux of $^{14}CO_2$, which was released during the decarboxylation of malate and pyruvate (Pärnik et al. 1988). Such a loss of $^{14}CO_2$ at low light intensities was the reason why the CO_2 uptake rate obtained during short-pulse labeling was nearly twice that obtained during long exposures. At high light intensities, which favored the reduction of 3-PGA, the uptake of labeled bicarbonate was depressed by only 20%. At the low light intensity, a marked proportion of the label also appeared in serine, which can be formed via 3PGA and oxypyruvate by reversed reactions of the glycolate pathway (Lawyer et al. 1982). In strong light, serine and glycine could also be synthesized via the glycolate cycle which could have started with the transketolase reaction. Although the experiment was carried out at a high bicarbonate concentration (30.3 mM), oxygenation of ribulose-1,5 biphosphate was ruled out.

After a 10 min pulse, leaves retained 45% of the tracer if illuminated, and 38% if kept in the dark. During a 2 min photosynthetic exposure, the label was incorporated mainly into 3 PGA, sugar phosphates and sugars (Fig. 4). Only 2 to 3% of the radioactivity of the water- and alcohol-soluble fraction appeared in C_4 -dicarboxylic acid. During the subsequent pulse-chase, the label from 3PGA and sugar phosphates was incorporated into sugars and the radioactivity of glycine and serine also increased. Such kinetics might have been the result of the synthesis of these compounds in the glycolate pathway initiated by the transketolase reaction. The decrease in radioactivity of the leaves in the light was probably caused by decarboxylation of glycine. After the pulse-chase in the dark (Fig. 4b), an increase in the percentage of the label in sugars was discovered. This was due to a decrease in the total content of the tracer and the absolute radioactivity of the sugars remained unchanged. This indicates that $^{14}CO_2$ was released from intermediates of photosynthetic metabolism, not from end products. In the dark, $^{14}CO_2$ was produced mostly by decarboxylation of pyruvate (Pärnik et al. 1988) which is also a substrate for alanine synthesis. Radioactivity of this amino acid increased, both as a percentage of the total radioactivity and as an absolute amount of ^{14}C .

The experiments described above provided insights into the dynamic reversible regulation of the operation of the photosynthetic apparatus. Plants grown in the same habitat were subjected to varied environmental conditions during $^{14}CO_2$ exposure. We also compared plants adapted to different environments. Plants from different depths did not reveal any qualitative differences in their metabolism. During a 15 sec exposure under saturating light, ^{14}C was incorporated mainly into

3PGA and other intermediates of the reductive pentose phosphate cycle (Table 3). In a manner analogous to the short-term exposure experiments under low light intensity, the synthesis of sugars in deep-growing plants adapted to low levels of illumination decreased and incorporation of ^{14}C into alanine increased.

Adaptation of *Thalassodendron ciliatum* to its habitat also was studied with respect to flavonoid compounds and bound amino acids. The plants were collected from the same habitats as those for investigation of photosynthetic metabolism. The content of flavonoids in mature leaves was 1.5 mg and 15.8 mg per g dry weight, respectively, at depths of 0.5 to 1 m and at 33 m. Chromatographic analysis (Margna and Margna 1969) and UV-absorption spectra of separated components (Mabry et al. 1970) suggested that the two major flavonoids present are probably glucoside derivatives of the flavonols quercetin and kaempferol. The roles of these compounds as well as their relation in the regulation of carbon metabolism is unclear.

The content of bound amino acids in adult leaves, analyzed following acidic hydrolysis of proteins, was identical in plants from the two habitats (Table 4). The young leaves of deep-water plants were markedly lower in proline and cystein. Differences in the total amino acid content at different depths were negligible. Young leaves contained 1.44 times more bound amino acids than old leaves (Table 4).

Thalassodendron ciliatum belongs to the group of C_3 plants. However, the presence of a large proportion of heterotrophic cells in the photosynthetic assimilator (Fig. 1) suggests coordination of autotrophic and heterotrophic cell functions and does not exclude carbon assimilation in the dark period and its storage in the form of organic acids in large vacuoles of the heterotrophic cells. This is in agreement with the diurnal kinetics of pH of the sap shown by the heterotrophic cells. Despite the alkalinity of the seawater (pH 8.2 at 29°C), the pH of the sap is in the range of 5.6 to 6.1. Acidification of the sap in *T. ciliatum* takes place at dawn and in early morning, but not during the night (Fig. 5), which is distinct from the pattern shown by terrestrial plants. The pH changes during the daytime were possibly due to conversion of labile keto acids (e.g., oxaloacetic acid) accumulated in vacuoles at night to the stable compound malate, rather than to an increase in the concentration of acids in vacuoles, because their formation during photosynthesis under saturating light levels was slow (Table 2, 3). To investigate this process, leaves were incubated for 10.5 h in the dark in seawater containing $\text{H}^{14}\text{CO}_3^-$, leaves were then killed and the content of the labeled malate was determined. After 18 min of illumination, the label in malate comprised 17%, following 30 min 22% and after 180 min 26% of the total radioactivity (Fig. 5). Malate was probably synthesized from some intermediate which was not identified; during a 180 min light period, its relative content decreased from 52 to 33%. Because the total radioactivity of the leaves did not change, the products of the dark CO_2 fixation did not appear to readily switch into respiratory metabolism. After a 180 min illumination period, only 8% ^{14}C occurred in sugars and 2% in serine and glycine, intermediates of the glycolate pathway. $^{14}\text{CO}_2$ taken up in the dark was probably metabolized via malate in the light, accompanied by an increase in pH up to 6.1, a value characteristic of the heterotrophic cells at night (Fig. 5).

CONCLUSIONS

Thalassodendron ciliatum is a typical C_3 plant exhibiting photorespiratory metabolism characteristic of this group of plants. As distinct from classical terrestrial C_3 plants, leaves of *T. ciliatum* lack stomata, and 80% of the leaf volume is occupied by chlorophyll-free heterotrophic cells which respire at a rate reaching about 66% of the gross photosynthetic rate. Light intensity curves of photosynthesis indicate that environmental conditions most favorable for the plant lay in the range of 6 to 26 m in depth. In plants growing 33 m deep, the CO_2 photoassimilation capacity is much

reduced at high as well as at low light intensities. Plants from deep waters contain more flavonoids, potential inhibitors of the electron transport chain (Allakhverdiev et al. 1989). A peculiarity of *T. ciliatum* is the synthesis of an intermediate from bicarbonate in the dark, which is converted into malate during subsequent illumination. This is accompanied by acidification of the cell sap, with pH values reaching as low as 5.6. During the daytime, the pH of the sap of heterotrophic cells increases and, by the evening, reaches the value characteristic of the dark period.

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Table 1. $^{14}\text{CO}_2$ uptake and the concurrent O_2 release by *Thalassodendron ciliatum* leaves. $^{14}\text{CO}_3$ -2.20 m, 6.0 Bq·nmol $^{-1}$, temperature 27°C, exposure time 10 min.

Habitat	$\left[^{14}\text{CO}_2 \text{ uptake} \right]$ mmol $\text{CO}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$	$\left[\text{O}_2 \text{ release} \right]$ mmol $\text{O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$	$\left[\text{Ratio } ^{14}\text{CO}_2 \right]$
Cöetivy Island depth of 11m PAR 46 W·m $^{-2}$	0.18±0.03	0.060±0.010	3.0±0.9
Farquhar Island lagoon	0.19±0.03	0.072±0.010	2.6±0.8

Table 2. Incorporation of ^{14}C into photosynthates in *Thalassodendron ciliatum* leaves at low and high light intensity. H^{14}CO_3 -30.2 mM, 880 Bq·nmol $^{-1}$, temperature 27°C, pre-illumination 30 min.

	Radioactivity of photosynthates (% total)					
	0.15 W·m ⁻²			20 W·m ⁻²		
	Exposure time (sec)					
	35	105	500	35	105	500
3-PGA+sugar						
phosphates	18.7	30.0	17.3	72.5	61.5	29.3
Sugars	-	4.5	7.7	3.8	14.4	41.9
Glycine	4.1	5.7	4.6	1.5	2.4	4.6
Serine	14.3	12.3	12.1	2.2	3.2	5.9
Malate	14.0	9.0	14.0	3.5	3.3	3.8
Aspartate	27.4	17.0	22.8	8.9	6.6	4.3
Alanine	3.6	5.0	4.0	1.5	2.0	2.6
Glutamate	3.2	4.0	3.8	0.4	2.0	2.6
Organic acids	6.8	2.5	1.7	1.7	1.1	1.3
Remainder	7.9	9.2	11.0	4.0	4.8	4.4

Table 3. Incorporation of ^{14}C into photosynthates in *Thalassodendron ciliatum* leaves growing at different depths. H^{14}CO_3 -4,5 mM, 540 Bq·nmol $^{-1}$, temperature 26°C, PAR 28 W·m $^{-2}$, pre-illumination 30 min.

	Radioactivity of photosynthates (% total soluble fraction)								
	Aldabra Is.			Farquhar Is.		Cöetivy Is.			
	Exposure time (sec)								
	15	60	300	15	120	17	60	120	
PGA+sugar									
phosphates	76.9	39.1	5.1	94.5	62.8	95.7	75.4	70.3	
Sugars	8.3	37.7	73.2	2.2	25.1	-	8.9	13.5	
Serine ⁺									
Glycine	1.1	2.5	9.8	-	1.1	-	1.6	0.6	
Malate	-	3.1	-	1.0	0.9	-	-	-	
Aspartate	6.5	6.1	4.3	2.3	1.8	3.0	3.3	2.1	
Alanine	1.1	3.3	3.3	-	1.3	1.3	10.7	12.9	
Glutamate	-	5.4	0.7	-	2.5	-	-	0.6	
Unidentified	6.1	2.6	3.6	-	4.6	-	-	-	

Table 4. Content of bound amino acids in leaves of *Thalassodendron ciliatum* from shallow (0.5 m) and deep (33 m) water.

Amino acid	Concentration, mg per g dry weight \pm S.D.			
	Young leaves		Mature leaves	
	0.5 m	33 m	0.5 m	33 m
Aspartic acid	6.29 \pm 0.39	6.10 \pm 0.18	4.34 \pm 0.16	4.36 \pm 0.18
Threonine	2.60 \pm 0.16	2.62 \pm 0.09	1.75 \pm 0.03	1.68 \pm 0.02
Serine	2.70 \pm 0.10	2.90 \pm 0.10	1.99 \pm 0.13	1.83 \pm 0.03
Glutamic acid	9.27 \pm 0.27	8.46 \pm 0.33	6.39 \pm 0.27	5.42 \pm 0.11
Proline	6.44 \pm 0.73	3.35 \pm 0.26	0.32 \pm 0.09	3.03 \pm 0.31
Cysteine	2.49 \pm 0.31	0.98 \pm 0.05	1.51 \pm 0.16	1.19 \pm 0.11
Glycine	3.93 \pm 0.10	4.16 \pm 0.17	3.27 \pm 0.17	2.61 \pm 0.09
Alanine	3.70 \pm 0.13	3.64 \pm 0.12	2.49 \pm 0.09	2.48 \pm 0.01
Valine	4.43 \pm 0.17	1.09 \pm 0.14	2.85 \pm 0.06	3.07 \pm 0.15
Methionine	1.74 \pm 0.31	1.08 \pm 0.02	0.69 \pm 0.13	0.81 \pm 0.02
Isoleucine	2.81 \pm 0.02	3.10 \pm 0.08	2.07 \pm 0.05	2.18 \pm 0.17
Leucine	4.72 \pm 0.01	5.13 \pm 0.16	3.43 \pm 0.06	3.34 \pm 0.04
Tyrosine	2.12 \pm 0.14	2.15 \pm 0.10	1.74 \pm 0.22	1.85 \pm 0.10
Phenylalanine	3.83 \pm 0.13	3.69 \pm 0.03	2.62 \pm 0.33	0.91 \pm 0.29
Histidine	2.02 \pm 0.01	1.81 \pm 0.04	1.30 \pm 0.10	1.43 \pm 0.09
Tryptophane	-	0.37 \pm 0.37	0.21 \pm 0.21	-
Lysine	4.17 \pm 0.41	4.22 \pm 0.04	4.13 \pm 0.25	3.74 \pm 0.16
Arginine	4.81 \pm 0.17	4.22 \pm 0.04	4.13 \pm 0.25	3.74 \pm 0.16

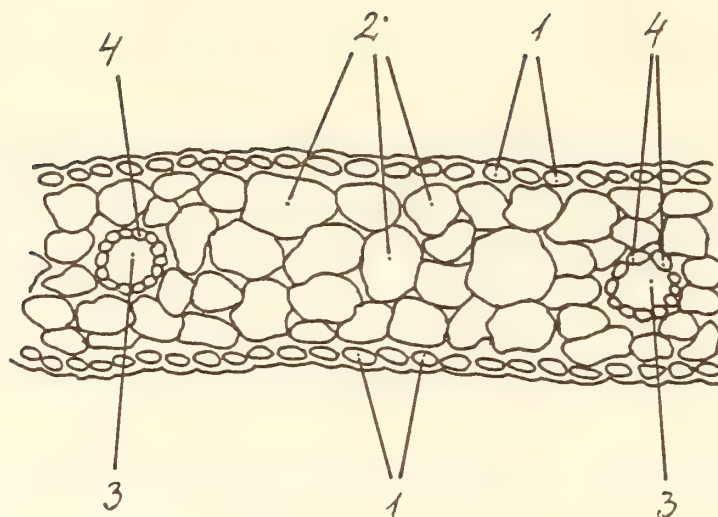


Figure 1. Cross-section of the leaf of seagrass *Thalassodendron ciliatum*.

- 1 - epidermal cells
- 2 - colorless vacuolized cells
- 3 - vascular bundles
- 4 - mestome sheath cells.

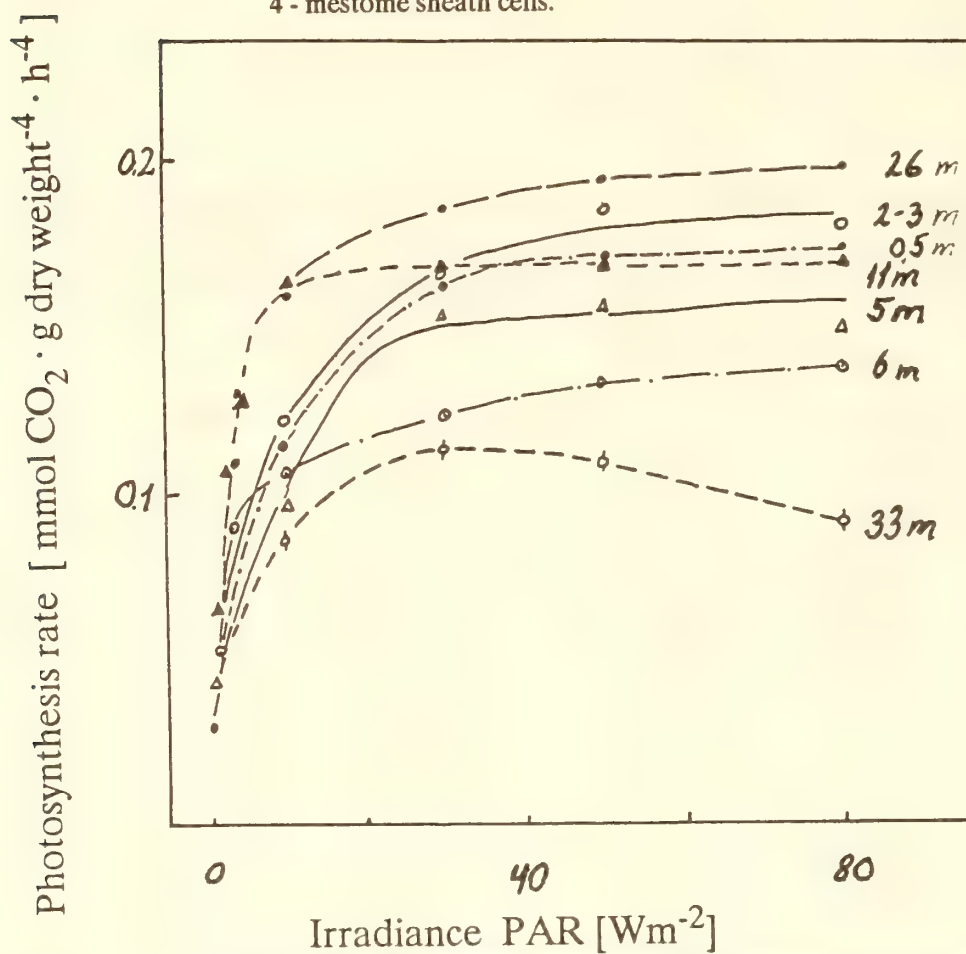


Figure 2.

Dependence of photosynthesis on irradiance in *Thalassodendron ciliatum* leaves growing at different depths. $\text{H}^{14}\text{CO}_3^-$ 2.02 mM, 6.0 Bq·nmol⁻¹, temperature 27°C, exposure time 20 min.

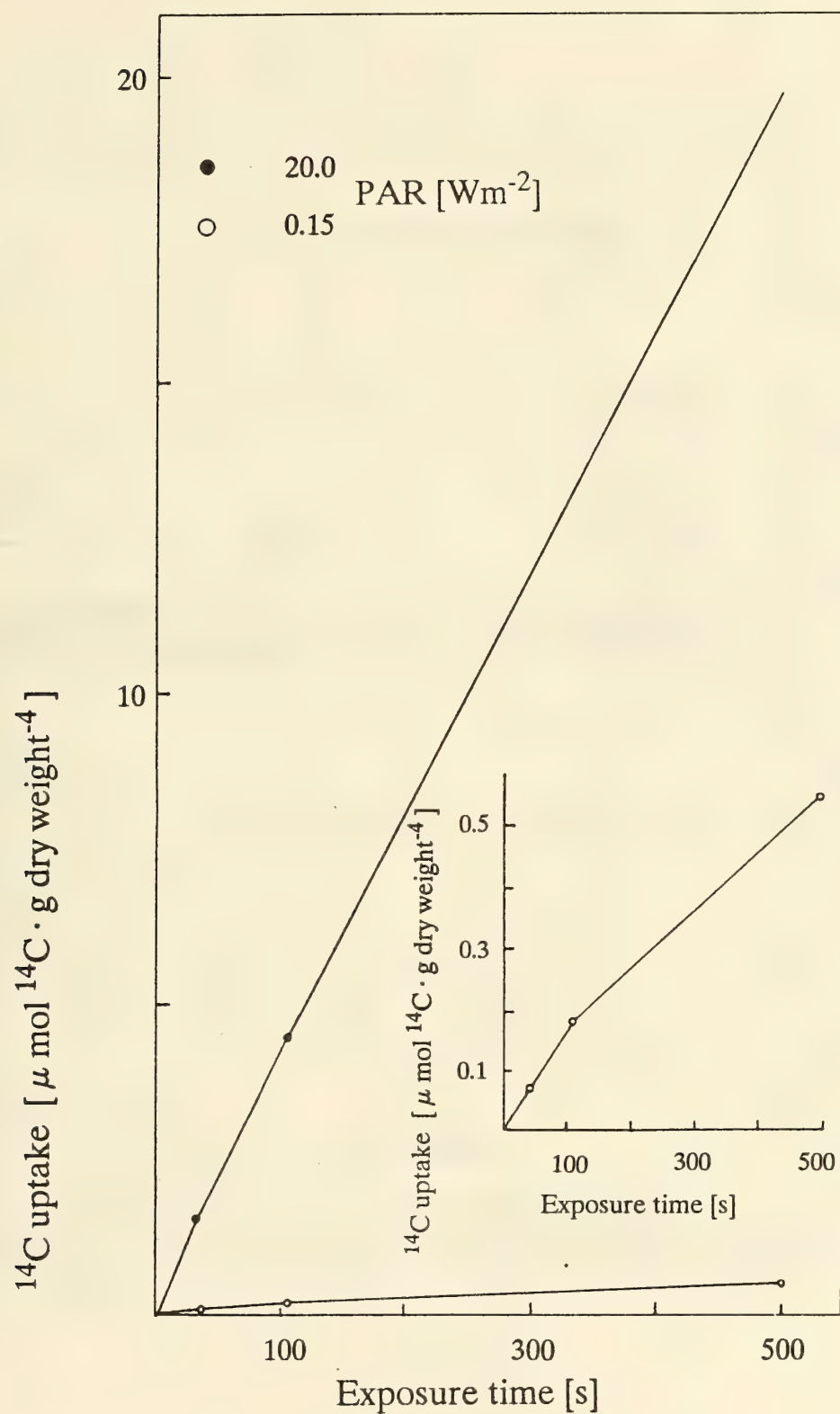


Figure 3. Kinetics of the ^{14}C uptake by *Thalassodendron ciliatum* leaves under limiting (PAR 0.15 $\text{W} \cdot \text{m}^{-2}$) and saturating (PAR 20 $\text{W} \cdot \text{m}^{-2}$) irradiance. $\text{H}^{14}\text{CO}_3^-$ 30.2 mM, 880 $\text{Bq} \cdot \text{nmol}^{-1}$, temperature 27°C, pre-illumination 30 min.

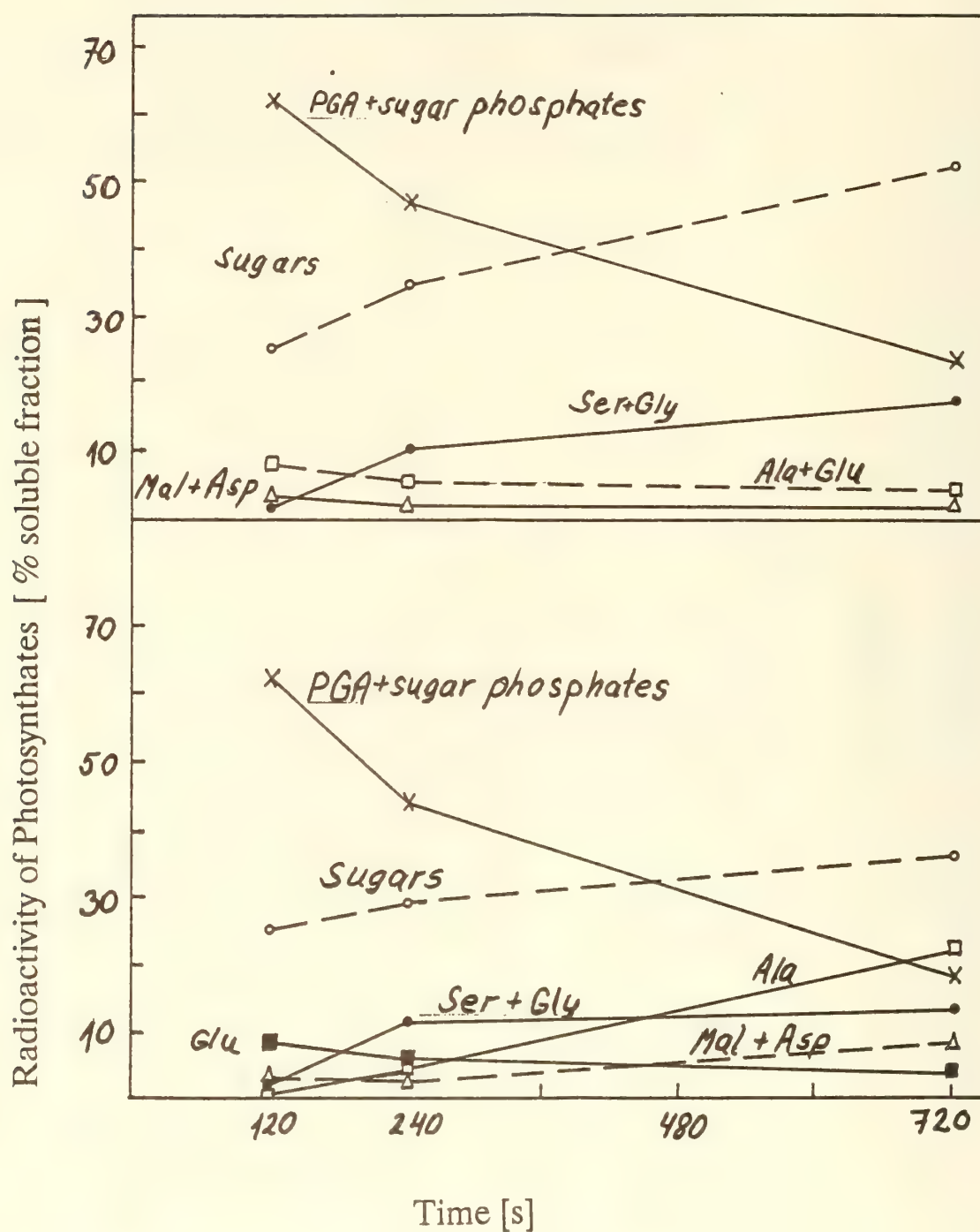


Figure 4.

Pulse-chase of ^{14}C assimilated during a 120 sec exposure to $\text{H}^{14}\text{CO}_3^-$ in the light (A) and in the dark (B). $\text{H}^{14}\text{CO}_3^-$ 4.5 mM, 540 Bq·nmol $^{-1}$, temperature 26°C, PAR 28 W·m $^{-2}$.

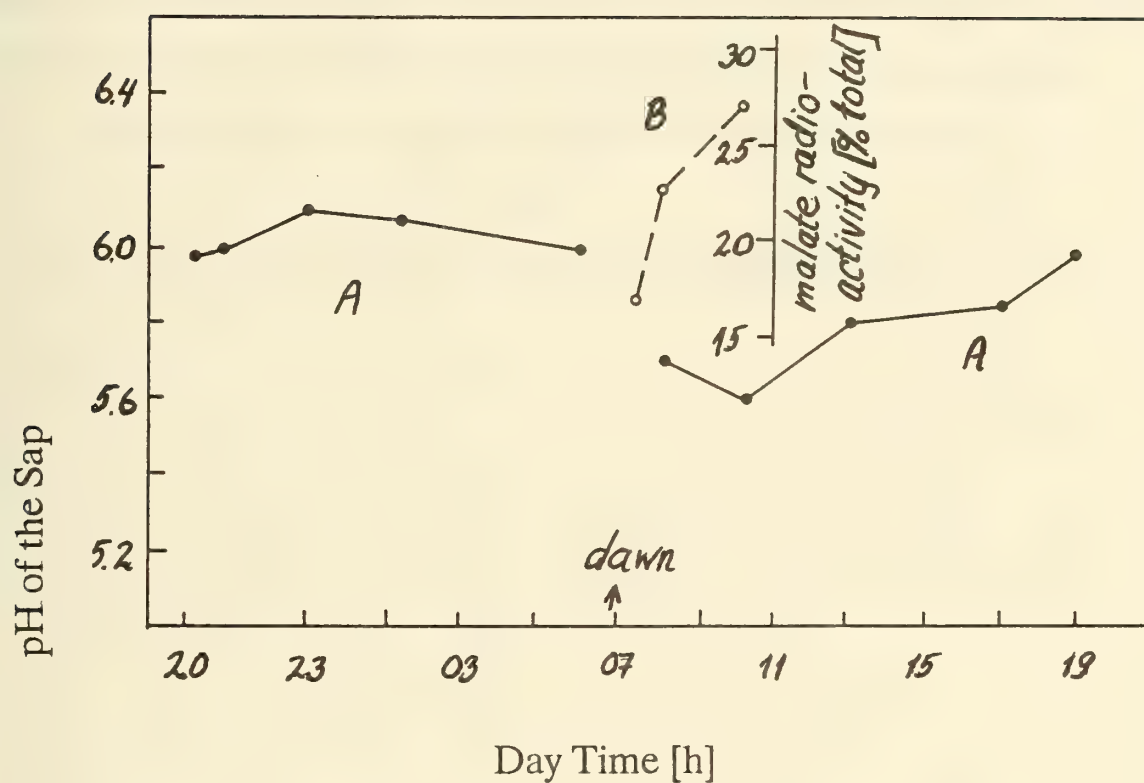


Figure 5. Diurnal kinetics of sap pH of the heterotrophic cells (A) in *Thalassodendron ciliatum* leaves and of ^{14}C incorporation into malate (B) from $\text{H}^{14}\text{CO}_3^-$ assimilated in the dark during 10.5 h.

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CHAPTER 13

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FROM DIFFERENT DEPTHS OF THE SEYCHELLES ISLANDS**

BY

K. Y. BIL', P. V. KOLMAKOV AND L. MUSCATINE

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INTRODUCTION

In the world ocean, there is a large group of symbiotic organisms substantially contributing to the total primary productivity of tropical shelf ecosystems (Davies 1977, Porter 1980, Falkowski et al. 1984, Sorokin 1986), in conjunction with macrophytic algae, seagrasses and phytoplankton. This group is the reef-building corals - symbiotic organisms including the polyps of colonial Cnidaria with their endosymbiotic microalgal zooxanthellae. It is known that zooxanthellae provide photosynthetic products not only to themselves but also for the host polyps (Land et al. 1975, Muscatine et al. 1981, Muscatine et al. 1984, Falkowski et al. 1984, Sorokin 1986). However, there are few data in the literature as to the type of photosynthetic carbon metabolism in zooxanthellae and possible changes under the effects of various environmental factors. Only several reports characterizing the type of photosynthesis in endosymbionts are available. In particular, Benson et al. (1978) and Hofmann and Kremer (1981) argue that zooxanthellae fix CO_2 through the C_3 pathway, i.e., carbon photoassimilation occurs with the help of ribulose-1, 5-biphosphate carboxylase and the first stable assimilate is 3-phosphoglycerate. Other works (Ting 1976, Beardall et al. 1976, Trench and Fisher 1983, Tyler and Trench 1986), on the contrary, showed that free-living dinoflagellates and coral zooxanthellae have high levels of phosphoenol-pyruvate carboxylase and malate dehydrogenase activity, and express the opinion that C_4 photosynthesis or mixed C_3 - C_4 pathways of photosynthesis are possibly present.

In the present work, we report the results of investigations of CO_2 assimilation rates and the composition of primary and final assimilates in coral zooxanthellae from various depths. The experiments were carried out during the Soviet-American expedition aboard the R/V Akademik A. Nesmeyanov.

METHODS AND MATERIALS

The symbiotic reef-building corals *Stylophora pistillata* (Ester) and *Seriatopora coliendrum*, inhabiting 2-3 m and 36 m depths near Desroches and Praslin Islands (Amirantes and Seychelles Groups), were chosen as the subjects of investigation. Depending on the experiment, fragments of coral colonies or isolated zooxanthellae were used. Zooxanthellae were isolated by the water-pick .TB.6"

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method (Johannes and Wiebe 1970). Polyp tissue was washed by seawater for 1-3 min to separate zooxanthellae from the polyps and fragments of coral skeleton. Zooxanthellae were isolated from the supernatant by precipitation at the repeated centrifugation force of 1500-2000 g), then washed in seawater from the polyp tissue residues. Cleaned zooxanthellae were resuspended in seawater at a concentration of 7.7×10^6 cells per ml. We controlled the purity of fractions and counted cells using a standard compound microscope. ^{14}C was used in the form of bicarbonate dissolved in seawater or as gaseous $^{14}\text{CO}_2$ for measuring photosynthetic rates and determining the composition of carbon metabolism products. Zooxanthellae cells were precipitated on 2.4 cm GF/A (USA) glass microfiber filters which were incubated for a fixed time in the exposure chamber with radioactive carbonic acid of bicarbonate. Carbon accumulation rates during photosynthesis were measured at light energies of $50\text{-}80 \text{ W}\cdot\text{m}^{-2}$, at air and water temperatures of 28°C after 10-30 sec pre-illumination of samples. After the exposure to light with radioactive bicarbonate, the samples were fixed by 1 ml of boiling 80% ethanol (EtOH) with formic acid added. The fixed zooxanthellae, together with the glass filters, were ground to homogeneous conditions and analyzed as well as another sample from the coral fragments. The analysis of the assimilate composition from the EtOH-soluble fraction was made using the method of two-dimensional ascending paper chromatography (Benson et al. 1950, Bil' et al. 1981, Bil' 1988). The mixture of butanol, formic acid and distilled water (75:13:12) and water-saturated phenol were used as solvents. Radioactivity of identified assimilates was measured by scintillation counter (Intertechnique, SL-30-300 type) and expressed in percentage of the total radioactivity of all assimilates eluted from the chromatograms.

RESULTS

Photosynthetic rates of isolated zooxanthellae from *Stylophora pistillata* and *Seriatopora coliendrum* obtained at saturating light and optimum temperatures are presented in Table 1. When CO_2 was used as the carbon source, the photosynthetic intensity was 1.5 to 2 times lower than with bicarbonate as the carbon source. However, the increase of CO_2 concentration in the exposure chamber leads to a considerable increase of the rate of ^{14}C assimilation (see experiment 2 in Table 1).

The analysis of primary assimilate composition produced by isolated zooxanthellae and zooxanthellae in polyps shows that these photoautotrophic organisms possess the typical C_3 -pathway of photosynthesis. In particular, during a short-term photosynthetic duration (5-15 sec), up to 90-94% of the radioactive carbon from the EtOH-soluble fraction of zooxanthellae is incorporated into 3-phosphoglycerate and other phosphatesters (Table 2). At longer exposures of cells in the radioactive medium, ^{14}C appears in the free sugars, fructose, glucose and saccharose. Intermediate assimilates typical of the C_4 pathway, such as malic and aspartic acids, appear in traces during short-term exposures to light. Such kinetics of carbon transformation during photosynthesis can be observed at various intensities of light flux, environmental temperatures and habitat depths.

It is known that one of the products of photosynthesis in zooxanthellae is glycerol (Muscatine 1980, Schlichter et al. 1983, Schlichter et al. 1984, Battey and Patton 1984). Glycerol was observed in the present study, not only after long-term exposures of zooxanthellae (see Table 3), but even at 5-15 sec where up to 7-8% of the ^{14}C from the EtOH-soluble fraction was incorporated into this assimilate (Table 2). The results presented in Table 2 also suggest that ^{14}C is consecutively transformed from 3-phosphoglycerate into free sugars and glycerol. However, after 15-sec long photosynthetic exposures to $^{14}\text{CO}_2$, where zooxanthellae were kept under a normal atmosphere in the dark, we observed an increase in the concentration of radioactive label in alanine, aspartate and glutamate. Radioactive carbon appears also in malate. In these experimental variants, free sugars were nearly absent but the concentration of ^{14}C -glycerol increased (Table 2). The results obtained are consistent with the data from Table 3 which shows that coral zooxanthellae (both isolated and in polyps) from the 36 m depth synthesize 2 to 2.5 times fewer free sugars than corals from depths of 2-3 m. In deep water coral

zooxanthellae, glycerol concentration also is greater (Table 3). As in the case of dark specimens (see Table 2), radioactive alanine, aspartate, glutamate and malate also increase. The form of carbon substrate (HCO_3^- or CO_2) does not substantially affect the ^{14}C -distribution among photosynthetic products, both in shallow - and deep-water samples (Table 3).

DISCUSSION

It is known that the photosynthetic products of zooxanthellae are quite diverse and in addition to carbohydrates they include such low molecular intermediates as 3-phosphoglycerate, phosphate esters, alanine, aspartate, glutamate, glycine and serine, fatty acids and many lipids (Muscatine and Cernichiaro 1969, Schmitz and Kremer 1977, Patton et al. 1977, Blanquet et al. 1979). The main insoluble carbohydrates of zooxanthellae are glucose and glycerol (Muscatine and Cernichiaro 1969, Muscatine 1980, Tables 2 and 3). Recently, it was reported that in the intact coral *Acropora scandens*, mannose may be a dominant carbohydrate. But since this polysaccharide had not been found earlier as a photosynthetic product of zooxanthellae, then its discovery by Schmitz and Kremer (1977) may be the result of interactions between the algae and polyps.

Our experiments on the dynamics of carbon accumulation and redistribution of ^{14}C among primary assimilates produced by zooxanthellae of *Stylophora pistillata* and *Seriatopora coliendrum* support the point of view of Benson et al. (1977) and Hofmann and Kremer (1981) that symbiotic dinoflagellates have the typical C_3 -pathway of photosynthesis. One can surmise that despite the presence of high concentrations of inorganic carbon in the form of bicarbonate, zooxanthellae prefer to photoassimilate carbon in the form of CO_2 (Table 1). However, it is not excluded that zooxanthellae, as well as *Chlorella* (Aizawa and Miyachi 1979), are capable of fixing carbon either in the form of CO_2 or bicarbonation depending on the long-term effects of certain factors.

As was mentioned above, the products of zooxanthellae photosynthetic carbon metabolism are hexoses and glycerol (Tables 2 and 3). After photoassimilation of ^{14}C -carbon dioxide directly in zooxanthellae, radioactive label is also quickly incorporated into fatty acids (Latyshev, unpublished data) or into esterified lipid drops (Muscatine and Cernichiaro 1969, Patton et al. 1977, Blanquet et al. 1979). ^{14}C -distribution between assimilate fractions in zooxanthellae, both in vivo and in vitro, depends to a large extent on conditions of light incubation and/or coral habitat. For example, Schmitz and Kremer (1977) found a high ^{14}C fixation in vivo in EtOH-soluble assimilates. However, pulse-chase experiments showed the rapid transformation of soluble compounds into insoluble ones. In a number of experiments (Schmitz and Kremer 1977), about 50% of the ^{14}C was found in the lipid fraction. In other experiments (Patton et al. 1977, Blanquet et al. 1979, Trench 1979), a considerable labeling of lipids also was obtained using isolated zooxanthellae following a long incubation in host tissue. This is to be expected, since corals and their symbiotic associations are rich in reserve and structural lipids. Some coral tissues, for example, can contain more than 34% lipids per unit dry weight (Patton et al. 1977), and the coral *Goniastrea retiformis* contains up to 3 mg of wax ester (cetyl palmitate) per cm^2 of tissue surface (Benson and Muscatine 1974). The ratio of hexose and glycerol, to our experience, depends considerably upon the light history; zooxanthellae from deep-water corals (Table 3) synthesize chiefly glycerol. In such low-light conditions, a substantial portion of ^{14}C also is shunted away from the Calvin-Benson cycle to synthesize alanine, aspartate, malate and glutamate. Contrastingly, in corals from 2-3 m in depth, the amount of radioactive carbon in C_4 -dicarboxylic acids and glycerol decreases, while it increases in free sugars (Table 3).

Since ^{14}C -glycerol can be found even after only 5-15 sec of photosynthesis (Table 2), its formation is most likely conditioned by reduction of a part of dihydroxyacetonphosphate into glycerol-3-phosphate by glycerol phosphate dehydrogenase ferment, with its further phosphatase hydrolysis to glycerol (Fig 2). One can suppose that if a coral dwells at a considerable depth, glycerol on the one hand promotes

osmotic regulation of cells, and on the other hand it is a main product of energetic transport from zooxanthellae to the polyp body. Glycerol not only provides for glycolysis and gluconeogenesis reactions but it also may be one of the precursors of membrane lipids, such as phosphoacylglycerol and 3-acylglycerol. It should be noted that for symbiotic organisms such as corals, we can only generalize about probable distributions of photosynthetic products between the producer and host, which depends to a great extent on specific habitat conditions.

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Table 1. Photosynthetic rates of zooxanthellae isolated from *Stylophora pistillata* and *Seriatopora coliendrum* depending on carbon substrate and habitat depth. Concentration of various carbon forms was: 1 - *Stylophora pistillata* - HCO_3^- - 6.5 mM, CO_2 - 0.105 mM; 2 - *Seriatopora coliendrum* - HCO_3^- - 18.0 mM, CO_2 - 0.194 mM. * value in parentheses = values of photosynthetic intensity at CO_2 - concentration of 0.56 mM.

Coral species and habitat	Depth m	Photosynthetic rate, $\mu\text{g CO}_2 \cdot 10^{-6} \text{ cells} \cdot \text{h}^{-1}$	
		Substrate	
		HCO_3^-	CO_2
<i>Stylophora pistillata</i> (Desroches)	2	28.3±3.0	14.9±1.5
<i>Seriatopora coliendrum</i> (Praslin)	3	13.5±1.5	9.7±1.0 (25.0±2.6*)
	36	11.3±1.2	7.4±0.8 (17.6±1.8)

Table 2. Composition of photosynthetic products of zooxanthellae and colony fragments of *Stylophora pistillata* from 2 - 3 m depth (Desroches). "Glycerol" includes glycerol and glycerol-3-phosphate, "Sugars" includes saccharose, glucose and fructose; (l) = light, (d) = dark; (-) = absence or traces of elements; → - transition of a sample from $^{14}\text{CO}_2$ $^{12}\text{CO}_2$. Relative deviations: for values higher than 10 - 5-10%, lower than 10 - 15-20%.

Sample	Duration (sec) of light incubation		Radioactivity of elements of EtOH-fraction in % of total radioactivity of eluates						
			Phosphate						
	$^{14}\text{CO}_2$	$^{12}\text{CO}_2$	esters	Sugars	Alanine	Aspartate	Glutamate	Malate	Glycerol
Isolated zooxanthellae	5		93.2	-	-	-	-	-	6.8
	15		91.1	-	-	-	-	-	8.1
	60		25.3	47.9	-	1.4	0.8	-	24.6
	180		15.5	68.0	0.6	1.0	0.6	-	14.3
	15	→ 60(l)	27.0	56.1	-	1.1	1.1	-	14.8
	15	→ 180(l)	7.8	67.6	-	1.0	2.0	-	21.6
	15	→ 60(d)	42.8	0.2	4.5	7.8	10.3	2.3	32.7
	15	→ 180(d)	32.7	-	3.7	13.3	25.0	2.5	22.8
Corals	60		32.9	57.6	-	-	-	-	9.5
	180		17.3	72.1	-	1.5	1.6	-	7.5

Table 3. Composition of products of 300 s photosynthesis in isolated zooxanthellae and colony fragments of *Seriatopora coliendrum* with reference to habitat depth (Praslin). Experiments were performed at saturating light at water and air temperature of 28° and concentration of $\text{CO}_2 = 0.48 \text{ mM}$, $\text{HCO}_3^- = 18.0 \text{ mM}$. Relative deviation: for more than 10 - 5-10%, less than 10 - 15-20%.

Sample	[Carbon- substrate]	Depth m	Radioactivity of elements of EtOH-fraction in % of total radioactivity of eluates							
			Phosphate esters	Sugars	Serine+ Glycine	Alanine	Aspartate	Glutamate	Malate	Glycerol
Isolated zooxanthellae	CO_2	3	4.3	60.9	1.1	0.8	1.2	14.6	0.9	16.2
		36	7.2	22.1	1.0	3.3	10.5	12.4	4.0	39.5
	HCO_3^-	3	20.6	5702	1.3	0.4	1.0	11.0	0.3	8.2
		36	11.3	28.8	0.5	3.7	10.4	19.4	5.9	20.0
Corals	CO_2	3	6.3	51.0	4.5	2.7	3.8	7.8	1.4	22.5
		36	6.8	18.1	0.4	5.1	5.6	10.8	3.0	50.2

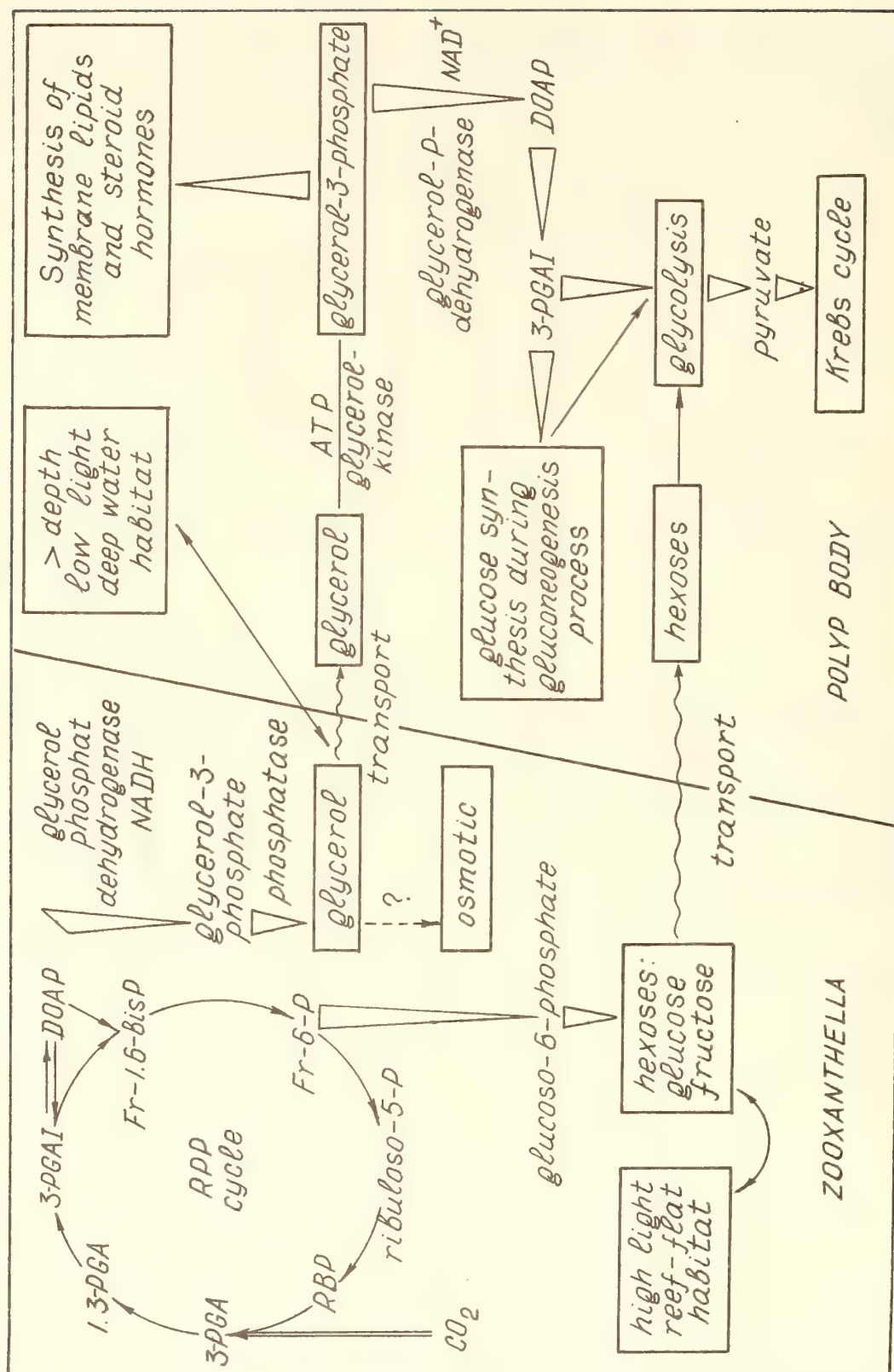


Figure 1. Photosynthetic products of zooxanthellae with reference to habitat depth and possible ways of their utilization by polyps.

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**CHAPTER 14
ESTIMATES OF INDIAN OCEAN PRODUCTIVITY
USING NATURAL FLUORESCENCE**

**BY
P. DUSTAN**

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CHAPTER 14
ESTIMATES OF INDIAN OCEAN PRODUCTIVITY
USING NATURAL FLUORESCENCE

BY
Phillip Dustan*

ABSTRACT

Measurements of the vertical distribution of phytoplankton natural fluorescence in the equatorial Indian Ocean produced estimates of oceanic productivity ranging from 70 to 150 mg C·m⁻²·day⁻¹. Vertical profiles of the water column revealed the presence of a distinct chlorophyll maximum which forms at or near the top of the thermocline at almost every station. Localized upwelling was observed in the vicinity of atolls which appears to be responsible for an island mass effect that may add to downstream oceanic productivity. There were no significant differences along an east and northward oceanic transect from 63° 20' E to 88° 56' E longitude. The estimates agree with previously reported production estimates for the Indian Ocean reinforcing the image of low and variable rates of production throughout the deep oceanic basin punctuated by localized island-induced upwellings.

INTRODUCTION

Phytoplankton productivity initiates the pelagic food chain and is an essential component of the "biological pump" which plays a regulatory role in the partitioning of carbon between the atmosphere and the sea. Studies of global change, the possibility of greenhouse warming, and advances in remote sensing of phytoplankton chlorophyll have increased the demand for field estimates of oceanic production in remote oceanic regions to verify modeling and provide "ground truth" information. The cruise track of the SAV89 Expedition to the Seychelles presented just such an opportunity for the equatorial waters of the Indian Ocean including the Seychelles Bank and atolls, and deep pelagic provinces. Additionally, information on the horizontal and vertical distribution of oceanic productivity might help to better understand the distribution of coral reef communities characteristic of the oligotrophic tropical waters of the Seychelles.

The Indian Ocean has not received the intense study characteristic of the Atlantic and Pacific Oceans. A base map for northern Indian Ocean productivity that was compiled from all available expedition results by Kabanova (1968), showed a wide range of values throughout the ocean basin. The analysis emphasized differences driven by southwest and northeast monsoonal seasonality with the highest production estimates occurring along the nearshore waters of the Arabian peninsula, the Indian subcontinent and Southeast Asia. An extension of the work showed that the pelagic regions are extremely oligotrophic with values ranging from 36 to 90 gC·m⁻²·yr⁻¹ (Koblents-Mishke, Volkovinsky, and Kabanova, 1970). This communication adds to this body of information by providing productivity estimates for equatorial waters of the Indian Ocean including the Seychelles Islands.

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MATERIALS AND METHODS

The investigation used a newly developing technique of estimating primary production which is based on the in-situ optical properties of chlorophyll termed natural fluorescence. Phytoplankton natural fluorescence in the sea results from the solar-stimulated emission of chlorophyll *a* in a narrow band centered at 683 nm. It has been used as a means of assessing the distribution and biomass of oceanic phytoplankton, and most recently for the estimation of rates of gross primary production. The level of natural fluorescence is related to the rate of light absorption by Photosystem II, and calculations of GPP are based upon the assumption that the ratio of photosynthetic to fluorescence yields is a predictable function of light intensity (Kiefer et al 1989, Chamberlain et al. 1990). This new method is a passive, in-situ technique that does not interfere with the natural metabolism of the plankton and thus could possibly generate estimates of production that are different from those generated by traditional methodologies which rely on enclosed incubations.

Measurements of natural fluorescence (NF) were made with a prototype PNF300 natural fluorometer (Biospherical Instruments, San Diego, California). The instrument measures surface and submarine light levels (PAR), temperature, pressure (depth), and upwelling radiance at 683 nm. The spectral responsivity of the radiance sensor is closely matched to the spectral emission characteristics of chlorophyll. The natural chlorophyll fluorescence signal, termed Lu(chl), is the spectrally integrated radiance of a chlorophyll-like source (Chamberlain, et al 1989). The optical collector of the NF sensor views a conical volume of water beneath the instrument with an angle of acceptance of approximately 20 degrees. The calibrated instrument output is in units of $\text{quanta} \cdot \text{m}^{-3} \cdot \text{sec}^{-1}$, a volume function. Instrument output was recorded using a laptop computer (Zenith PC181).

The data were processed using software provided by Biospherical Instruments. Calculations included the diffuse attenuation coefficient, chlorophyll pigment concentration and production. Calculations of gross primary productivity (GPP) are reported in $\text{nmC} \cdot \text{m}^{-3} \cdot \text{sec}^{-1}$ to signify the instantaneous nature of the measurement (refer to Chamberlain et al. 1990). Estimates of integrated water column GPP were calculated using the depth-binned data (0-130m) which was normalized to the average surface irradiance of all casts and then combined with dawn-to-dusk sunlight data recorded during a coral observation experiment to provide estimates of daily water column production ($\text{mgC} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$).

Vertical profiling casts were carried out by hand lowering the instrument from a platform located on the port side of the ship approximately 2 m above the sea surface. Hand lowering was very efficient with the time for a complete cast from the surface to 200 m taking less than 15 minutes. Care was taken to position the ship with the sun in full view at an angle that would not cast the ship's shadow into the cast path of the instrument.

Fifteen stations were occupied during the cruise. Three stations were carried out west of the Maldiv Islands, three stations were within the Exclusive Economic Zone (EEZ) of the Seychelles, one while enroute from Aldabra to the coast of Africa, and a series of 8 stations transecting the Indian Ocean on the return passage from Mahé to Singapore. This return track sampled the waters of the eastward flowing Equatorial Countercurrent west and east of the Maldives, and then traversed northeast, sampling equator waters at 80° E and, lastly, encountered the waters of the westward flowing North Equatorial Current. Thus, when taken in their entirety, the oceanographic stations sampled waters of both the North and South Equatorial Currents and the countercurrent spaced between the two, between east longitude 14° to 89°. Hydrographic samples were collected with Nansen bottles at stations 8 through 15 allowing for a comparison of NF data with discrete chlorophyll, nutrient and some physical oceanographic data (Fig. 1, Table 1).

Nutrient and discrete chlorophyll analyses were carried out by scientists onboard the research vessel, principally Prof. Viktor G'old (chl), Luiza Propp (NO_2 , NO_3 , NH_4 , see Propp et al, Ch.7 this volume) and Yelena Chernova (PO_4 , Porganic, Si, see Novoshilov et al. Ch.2 this volume).

At Astove Atoll, in the southern waters of the Seychelles EEZ, a series of three vertical profiling casts were made from a small boat at distances of 200 m, 1.8 km, and 7.4 km from the island edge to investigate the island mass effect. A fourth cast, approximately 3 km to windward of Astove Atoll, was carried out from the R/V Akademik A. Nesmeyanov. An analysis of these data will be presented in greater detail in a forthcoming communication (Dustan, submitted).

RESULTS

Virtually every cast made in the open sea displayed a similarly shaped profile consisting of a sharp drop in natural fluorescence within the upper mixed layer, followed by a subsurface NF maximum at or near the top of the thermocline, usually between 20 to 50 m, followed by a rapid decrease in signal into deeper water (Appendix 1). Estimates of surface chlorophyll derived from natural fluorescence ranged between 0.06 and 1.23 $\text{mg}\cdot\text{m}^{-3}$. Chlorophyll concentration was significantly correlated with shipboard measurements made using in-vivo fluorescence ($r = .76$, $n = 43$, $P < 0.01$, Gol'd and Shatrov, unpublished, Table 2). Calculation of Kpar (diffuse attenuation coefficient for spherical irradiance) were consistently less than 0.1, often less than 0.06 at depths between 10 and 80 m (Appendix 1). Nutrient levels, especially nitrate and phosphate, were low, often below detection, in the surface mixed-layer. Deeper, levels were often elevated in the thermocline region (50 - 75 m) which coincided with the position of the subsurface NF maximum (Table 2).

Natural Fluorescence estimates of water column primary production range from 75 to 150 $\text{mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Fig 2). Oceanic stations within the Seychelles EEZ did not show an increase in production over deep ocean stations. Interestingly, the highest and lowest values occurred at stations 12 and 13, that were within 75 nm of each other just north of the equator at 80 E. There was no correlation between integrated water column production and the depth of the chlorophyll maximum layer.

Vertical profiles often showed differences in the water column structure between the down and upcasts of a single profile. Data from stations 4, 5, 13, and 15 exhibited vertical displacements of between 1 and 7 m between the down and upcasts in NF and temperature data. At stations 6 and 7, the vertical displacement was close to 30 m. These two stations occurred close to each other during a transit from Farquhar and Coetivity in over 3000 m with relatively calm conditions.

The profiles at Astove Atoll demonstrated how island mass can effect the vertical structure of the ocean. A thermal profile in ocean waters 7.4 km away from Astove Atoll showed a well-defined surface mixed-layer with a pronounced thermocline between 50 and 70 m (Fig. 3). This thermal structure was generally typical of profiles made in the Indian Ocean during this cruise (January to March 1989). The vertical distribution of temperature close to the Atoll revealed an upward intrusion of deeper cooler water into the surface waters on the upwind (upcurrent) side of the island platform (Fig. 3). There, the mixed-layer was poorly defined and the top of the thermocline was at approximately 30 m with a continuous decrease in temperature deeper. Closer to the atoll, just two hundred meters from the reef face, the temperature profile revealed a small temperature break at about 15 m and a more pronounced thermocline that began at 35 to 40 m.

On a SCUBA dive along the same reef face, divers experienced a series of temperature inversions as they descended through swirling water masses. A temperature profile obtained during

this dive by handcarrying the natural fluorometer revealed an overall decrease in temperature with depth but with numerous temperature reversals. Temperatures recorded close to the reef face were cooler by 1 to 2 °C (26 to 28 °C) than temperatures recorded 1-4 m away from the reef face.

The thermal profile in the wake of the atoll, 1.8 km from the reef, was more variable and the thermocline poorly defined (Fig. 3). Temperatures above 40 m were slightly cooler than the reef edge profile, and deeper they were slightly warmer to approximately 100 m, indicating strong vertical mixing and a breakdown of thermal stratification in the wake of the atoll.

The vertical distribution of gross primary production (GPP) at Astove Atoll tracked variation in the thermal profiles (Fig. 3). The ocean station revealed a typical pelagic surface mixed layer approximately 55 m deep. The GPP signal decreased with depth and there was a subsurface maximum between 60 and 75 m near the top of the thermocline. The station to windward of the atoll, with a shallowing thermocline, exhibited decreased GPP at the surface and a broad subsurface maximum considerably shallower than the oceanic station (40 m). Close to the reef, the signal was higher and displayed a subsurface maximum that peaked sharply at 40 m, the upper edge of the thermocline. Gross primary production 1.8 km offshore was similar to the reef station, with a pronounced subsurface maximum at 30 m that gradually decreased with depth. Production in the wake of Astove Atoll was slightly increased over oceanic values, although there was no replication of the casts due to time limitations.

Examination of a Coastal Zone Color Scanner scene (CZCS 79308082220.N17, November 4, 1979) processed for oceanic chlorophyll concentration revealed that phytoplankton chlorophyll concentrations in the region are low and range between 0.056 and 0.195 $\text{mg}\cdot\text{m}^{-3}$. The low values were confirmed by shipboard sampling where values ranged between 0.04 and 0.25 $\text{mg}\cdot\text{m}^{-3}$ between 0 and 50 m for oceanic samples and 0.1 to 0.36 $\text{mg}\cdot\text{m}^{-3}$ for atoll waters (Gol'd and Shatrov, unpublished). Thus while the imagery was not coincident with ship data, the pigment levels are in general agreement (Dustan, submitted).

DISCUSSION

Optical estimates of chlorophyll pigment concentration were consistently higher than shipboard estimates but within the levels expected for oligotrophic waters. The estimates were also consistent with bio-optical modeling of the diffuse attenuation coefficient (Smith and Baker 1978a, 1978b, Smith 1981) and satellite estimates of the region (Dustan submitted).

The estimates of integrated water column production in this report are in agreement with earlier published estimates of primary productivity that show the pelagic Indian Ocean to be oligotrophic. The range of values for daily production compare favorably to the lower end of the commonly accepted ranges for the Indian Ocean (Koblentz-Mishke 1970 in Lorenzen 1976, FAO 1976, Kinne 1982, Parsons and Takahashi 1984). There did not appear to be any consistent pattern to the spatial variability of production. Seemingly significant variations often occurred during stations or within short geographical distances indicative of oceanic mesoscale patchiness. Clearly more data are required to partition the variability between different oceanic provinces.

The vertical distribution of fluorescence showed a consistent maximum at or near the top of the thermocline. Nutrients, especially nitrate and phosphate, were frequently elevated in this depth range lending strength to the suggestion that the chlorophyll maximum layer forms in relation to the nutracline at the base of the mixed layer as suggested for other oceanic situations (Longhurst, 1981).

The vertical displacement of features during casts is consistent with the passage of internal waves

The vertical displacement of features during casts is consistent with the passage of internal waves beneath the vessel. The prevailing winds and currents result in a westward propagation of internal waves until they meet an island or platform where shallowing might result in the upward vertical transport of nutrients into the photic zone through a variety of physical mechanisms. Breaking internal waves embedded within the stratified water column would provide added energy for mixing (Wunsch, 1972) through microstructure billow turbulence (Woods and Wiley, 1972). Satellite observations (CZCS- Coastal Zone Color Scanner) reveal distinct chlorophyll plumes trailing off to leeward of Seychelles atolls (Dustan, submitted) and a general increase in chlorophyll over the entire northern island platform encompassing the northern granitic islands. Such an island mass effect (*sensu* Doty and Oguri, 1956) would be enhanced by rainfall and subsequent nutrient runoff in the high islands and would contribute significantly to the regional patchiness of phytoplankton production.

The data show that the reefs of the Seychelles Islands are bathed by clear oligotrophic waters having a relatively shallow thermocline, which combined with an island mass effect might help to explain the vertical depth distribution of corals on southern atolls. For example, at Astove Atoll, the corals ceased rather abruptly at approximately 30-45 m, even though the waters were very clear and algal species were abundant deeper. The episodic upward intrusion of cold water into the shallows would expose the reef community to temperatures close to or below their lower thermal tolerances, raising the possibility that the depth penetration of reef-building corals in the clear tropical waters of this region could be limited by low temperatures, not light availability.

The study of natural fluorescence by photosynthetic organisms in the sea is in its infancy. Natural fluorescence methodology may have application for rapidly assessing water column primary productivity when other more time consuming methods cannot be used. This could be most helpful in support of fisheries surveys and other sorts of environmental research where field support resources and time are limited.

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Table 1. Indian Ocean Productivity Stations Sampled During SAV89. Listing of station positions for vertical profiles. The station positions, in decimal degrees, were obtained using satellite navigation.

DATE	STATION	LATITUDE	LONGITUDE	LOCATION
5 JAN 89	1	02° 13.05'S	67° 21.00'E	EAST OF SEYCHELLES
6 JAN 89	2	02° 03.93'S	63° 59.70'E	EAST OF SEYCHELLES
7 JAN 89	3	03° 34.00'S	60° 15.00'E	EAST OF SEYCHELLES
30 JAN 89	4	07° 22.50'S	43° 36.37'E	OFF AFRICA
11 MAR 89	5	10° 05.85'S	47° 38.30'E	NEAR ASTOVE ATOLL
13 MAR 89	6	08° 09.70'S	54° 13.40'E	SEYCHELLES EEZ
13 MAR 89	7	07° 58.00'S	54° 03.50'E	SEYCHELLES EEZ
18 MAR 89	8	03° 04.30'S	63° 02.00'E	WEST OF MALDIVES
21 MAR 89	9	03° 04.20'S	77° 55.23'E	EAST OF MALDIVES
22 MAR 89	10	01° 05.15'S	81° 35.76'E	SOUTH OF EQUATOR
22 MAR 89	11	00° 01.40'N	81° 35.79'E	EQUATOR
23 MAR 89	12	01° 29.40'N	84° 46.40'E	NORTH OF EQUATOR
23 MAR 89	13	02° 34.90'N	85° 00.03'E	NORTH OF EQUATOR
24 MAR 89	14	04° 08.90'N	87° 45.00'E	NORTH OF EQUATOR
24 MAR 89	15	04° 47.26'N	88° 56.53'E	NORTH OF EQUATOR

Table 2. Nutrient and Chlorophyll data for Equatorial Crossing Transect. Chlorophyll values are presented as pnfChl which was determined optically using natural fluorescence with the PNF300 and CHL values were determined shipboard by Prof. Gol'd. An asterisk (*) represents data below detectable limits and an hyphen (-) represents no data available.

Date	Station	Depth m	nutrient concentrations in $\mu\text{g at.l}^{-1}$						P _{org} Si
			pnfCHL $\mu\text{g.l}^{-1}$	CHL $\mu\text{g.l}^{-1}$	NO ₂	NH ₄	NO ₃	PO ₄	
18 MAR 89	8	0	-	0.04	*	*	0.54	0.21	0.06
		10	0.14	0.02	0.03	0.50	0.43	0.20	0.341.98
		30	0.16	0.02	*	0.50	0.54	0.13	0.311.90
		50	0.81	0.50	0.03	0.83	0.70	0.23	0.402.85
		100	0.15	0.03	0.03	0.66	16.50	1.15	0.3512.4
21 MAR 89	9	0	-	0.08	0.03	0.23	0.55	0.15	1.372.25
		10	0.11	0.05	*	0.68	0.58	0.21	0.642.25
		30	0.14	0.08	0.07	0.97	0.54	0.07	0.542.00
		50	0.34	0.11	0.04	2.29	0.57	0.21	0.482.25
		100	0.21	0.07	0.06	0.53	15.64	0.90	1.461.50
22 MAR 89	10	0	-	0.04	0.03	1.76	0.65	0.32	* 1.75
		10	0.11	0.05	0.02	1.70	0.58	0.21	0.161.85
		20	0.125	0.09	0.03	0.56	0.55	0.15	0.491.50
		30	0.195	0.14	*	0.23	0.55	0.18	0.381.45
		50	0.775	0.17	0.05	0.38	1.62	0.29	0.322.63
		75	0.53	0.16	0.45	0.38	13.00	0.89	1.148.40
		100	0.24	0.10	0.07	0.23	15.00	1.03	0.961.25
22 MAR 89	11	0	-	0.05	0.03	0.38	0.70	0.15	1.741.50
		10	0.12	0.05	0.03	0.38	0.60	0.13	0.261.35
		20	0.12	0.04	0.03	0.38	0.54	0.11	0.111.45
		30	0.14	0.05	0.05	0.23	0.62	0.14	0.181.30
		50	0.21	0.08	0.02	1.11	0.61	0.21	0.261.35
		75	0.85	0.19	0.18	0.38	1.72	0.84	0.607.28
		100	0.32	0.10	0.12	0.53	15.58	1.10	0.79204.75
23 MAR 89	12	0	-	0.05	*	*	0.57	0.07	0.36 -
		10	0.09	0.04	0.03	0.20	0.57	0.13	0.37 -
		20	0.09	0.05	*	*	0.60	0.10	0.30 -
		30	0.13	0.05	*	*	0.61	0.15	0.09 -
		50	0.73	0.10	0.03	0.20	1.56	0.24	0.79 -
		75	0.69	0.25	0.27	0.20	7.33	0.58	0.48 -
		100	0.27	0.18	0.09	0.20	18.60	1.23	0.74 -

Table 2. Continued.

Date	Station	Depth m	nutrient concentrations in $\mu\text{g at}\cdot\text{l}^{-1}$						P _{org} Si
			pnfCHL $\mu\text{g}\cdot\text{l}^{-1}$	CHL $\mu\text{g}\cdot\text{l}^{-1}$	NO ₂	NH ₄	NO ₃	PO ₄	
23 MAR 89	13	0	-	0.05	*	*	0.38	0.07	0.13 -
		10	0.11	0.04	*	*	0.40	0.10	0.09 -
		20	0.1	0.06	*	0.50	0.36	0.09	0.13
		30	0.12	0.05	*	0.20	0.40	0.09	* -
		50	0.49	0.20	*	0.20	0.36	0.14	* -
		75	0.76	0.18	0.41	0.20	5.20	0.42	0.24 -
		100	0.4	0.11	0.1	0.40	16.10	1.18	0.37 -
24 MAR 89	14	0	-	0.05	*	*	0.50	0.07	0.40 -
		10	0.11	0.05	*	0.20	0.50	0.05	0.40 -
		20	0.13	0.06	*	*	0.48	0.07	0.08 -
		30	0.25	0.05	*	*	0.43	0.07	0.16 -
		50	0.84	0.25	0.42	*	3.20	0.35	0.23 -
		75	0.41	0.24	0.18	0.20	14.10	0.25	0.80 -
		100	0.17	-	0.03	0.40	-	1.55	0.50 -
24 MAR 89	15	0	-	0.09	*	0.20	0.53	0.06	0.13 -
		10	0.13	0.04	*	*	0.52	0.05	0.85 -
		20	0.13	0.05	*	*	0.50	0.03	0.02 -
		30	0.14	0.04	*	*	0.43	0.07	* -
		50	0.46	0.05	*	*	0.46	0.11	0.10 -
		75	0.96	0.20	0.27	0.40	7.90	0.60	0.15 -
		100	0.38	0.10	0.09	0.40	19.60	1.29	0.97 -

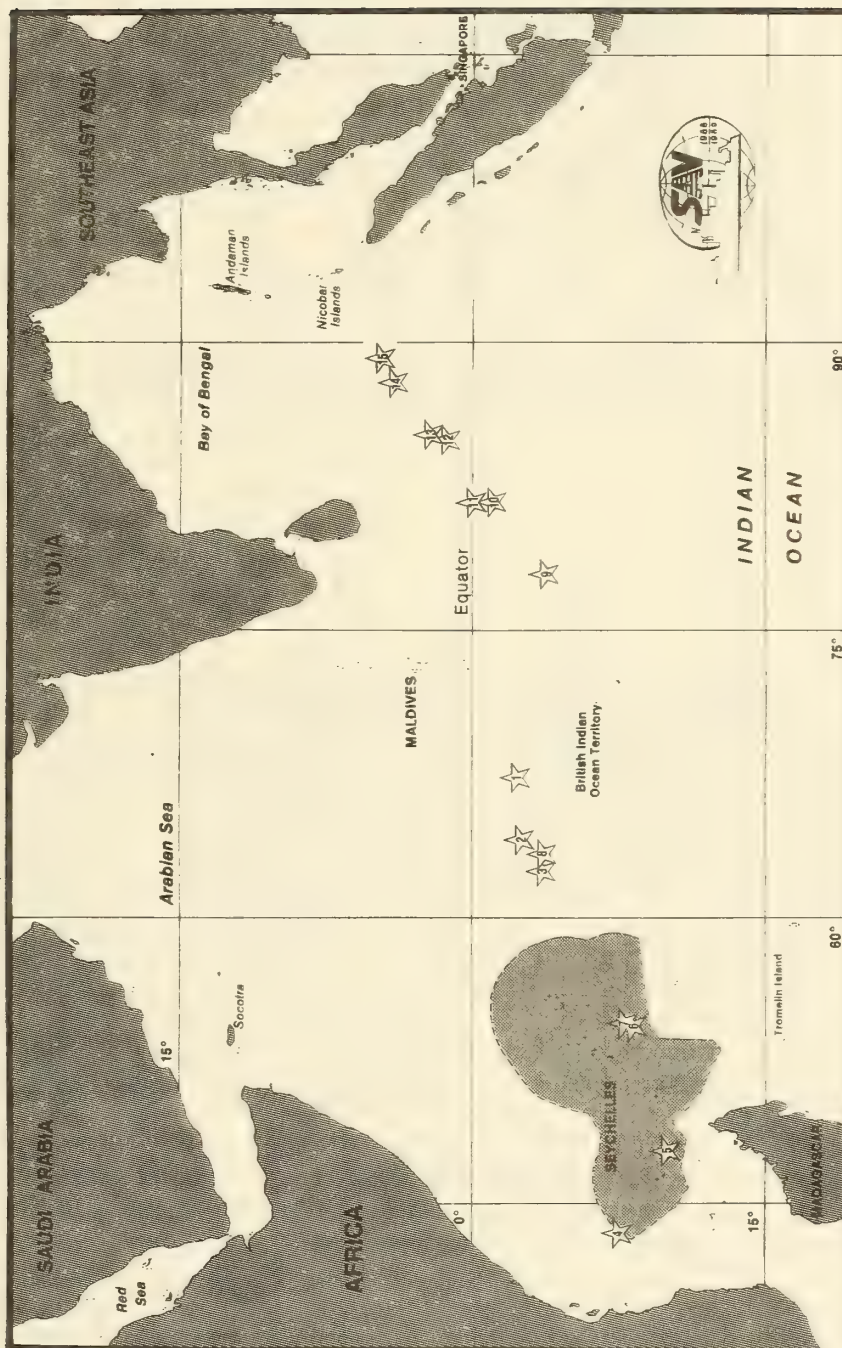


Figure 1. SA V89 station location map for vertical profiles. Station information is listed in Table 1.

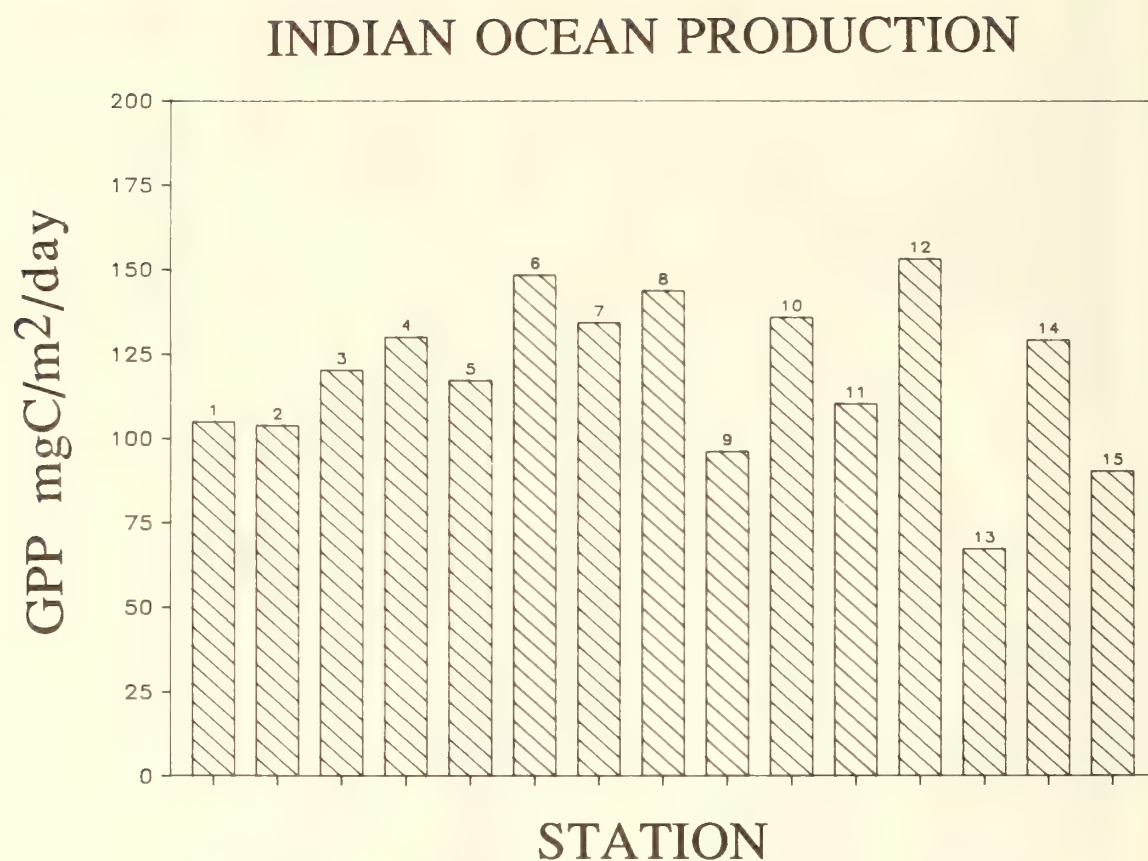


Figure 2. Integrated water column productivity for oceanic stations occupied during SAV. Estimates were derived from calculations of instantaneous in-situ gross primary production using natural fluorescence and dawn-to-dusk surface light conditions recorded at St. Joseph Atoll, Seychelles on 3 March 1989. See Materials and Methods for details.

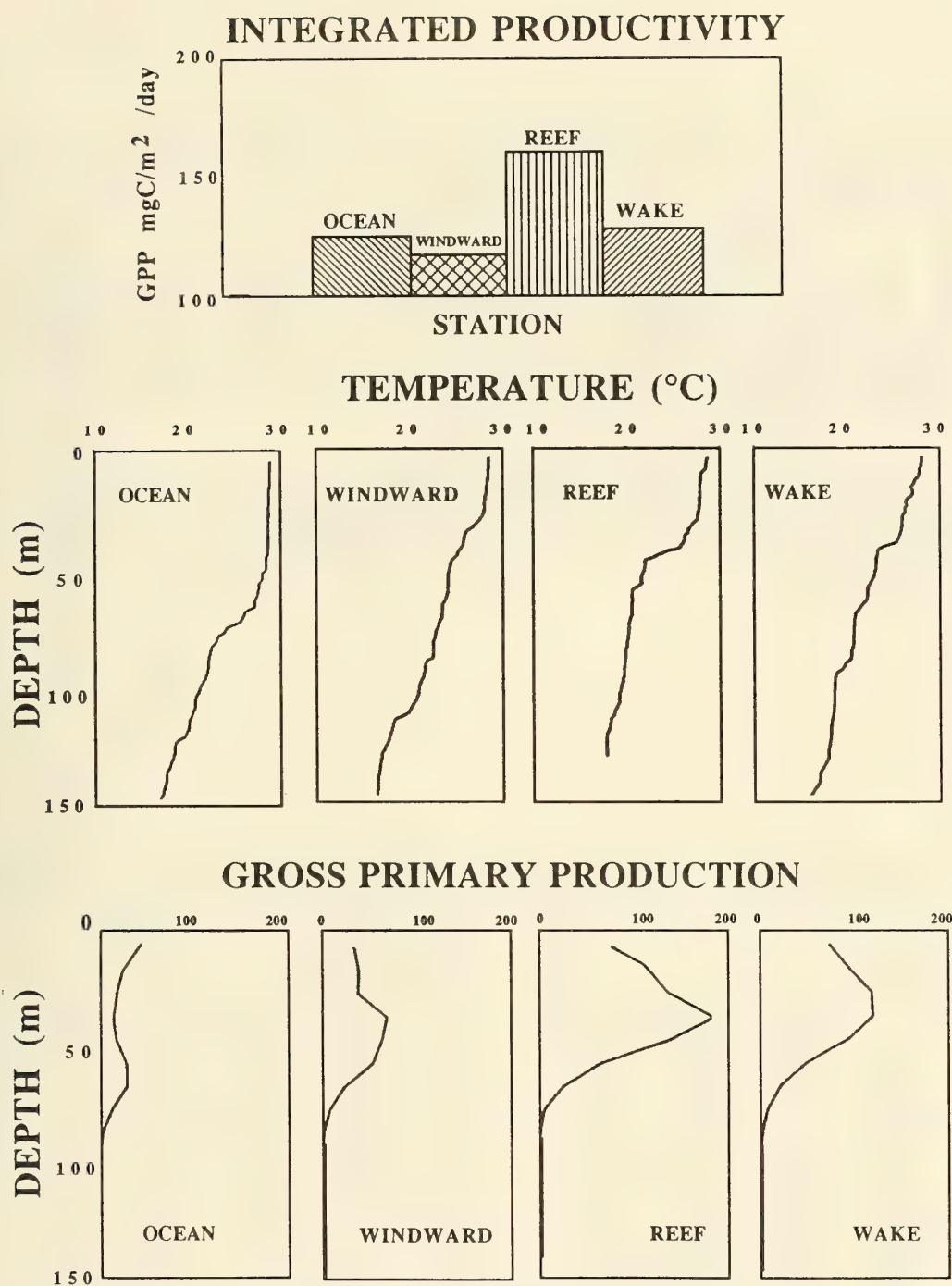


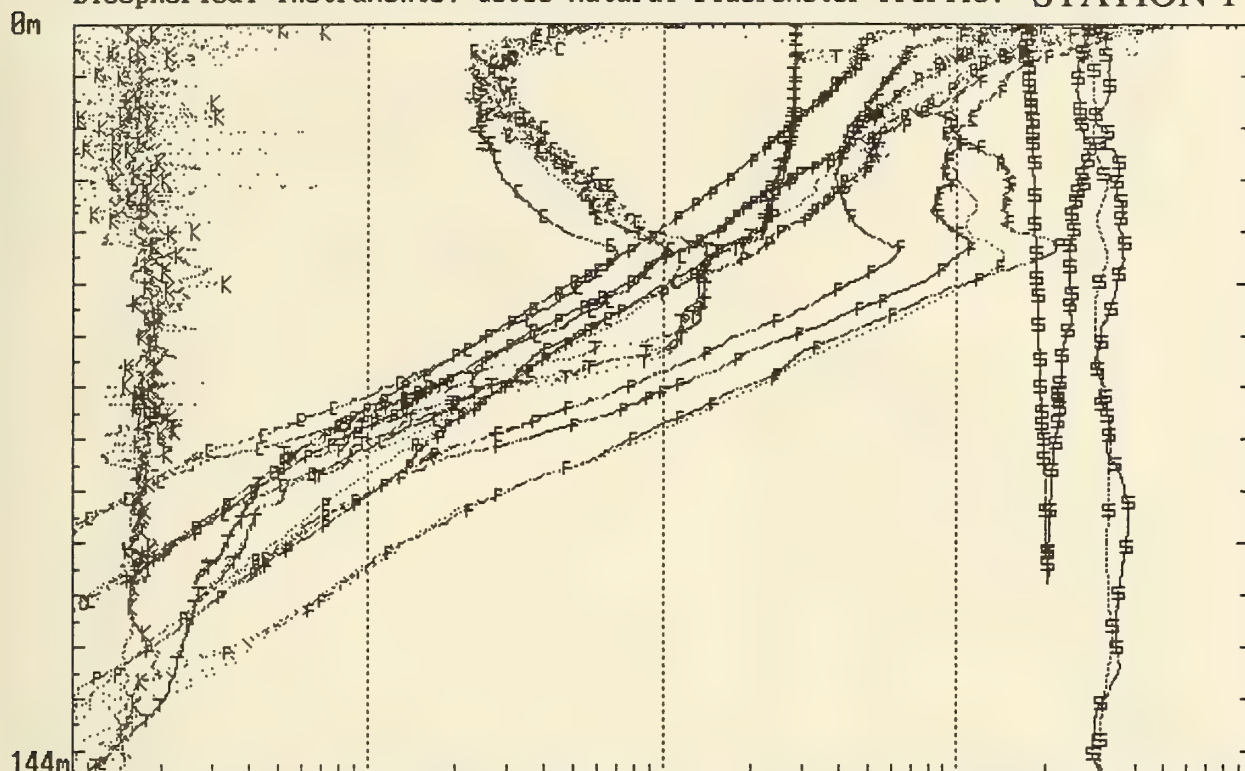
Figure 3. Island mass effect at Astove Atoll, Seychelles: Integrated water column productivity and vertical distribution of temperature and gross primary production. Upper bar chart shows integrated water column productivity normalized to identical surface light conditions recorded at St. Joseph Atoll, Seychelles on 3 March 1989. Vertical profiles of temperature and instantaneous in-situ gross primary production were recorded simultaneously using an Biospherical Instruments PNF Natural Fluorometer (PNF-300). See Materials and Methods for details.

APPENDIX

Data sheets for vertical profiles from stations 1-15. The graphical presentation of vertical distribution data plots all the points used in the software calculations. The variables are marked by letters that refer to the parameters listed in the legend of the horizontal axis. For example, the letter F refers to Natural Fluorescence and the letter T for Temperature.

The tabular presentation shows the data binned by depth. The coefficients used to calculate productivity and chlorophyll concentration are listed below the table. The reader is referred to Chamberlain et al. 1990 for details on calculation of GPP and chlorophyll.

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 1



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.6	853.791	1949.714	n.a.	n.a.	28.26°	35.519	93.5	
1.0 - 11.0	6.1	905.571	2417.734	0.067	37.46%	28.22°	15.043	32.9067	0.06 108.837
11.0 - 21.0	16.5	489.540	2352.866	0.057	20.81%	28.23°	7.855	27.7019	0.06 55.194
21.1 - 30.8	25.8	354.123	2632.597	0.053	13.45%	28.08°	8.751	38.7278	0.09 60.689
31.0 - 40.9	35.6	223.543	2686.735	0.061	8.32%	27.80°	9.715	59.8673	0.17 68.501
41.1 - 50.8	45.8	112.922	2566.200	0.070	4.40%	26.91°	10.363	91.7648	0.36 74.238
51.0 - 61.0	55.8	52.173	2488.994	0.071	2.10%	26.50°	4.583	55.6070	0.34 32.986
61.1 - 71.0	66.8	24.967	2407.073	0.064	1.04%	24.19°	1.730	24.3793	0.27 12.245
71.1 - 81.0	75.6	13.871	2442.486	0.065	0.57%	21.58°	0.745	11.3250	0.20 5.268
81.1 - 90.9	85.3	7.923	2539.658	0.058	0.31%	19.87°	0.276	4.3454	0.13 1.923
91.0 - 100.9	96.1	4.561	2679.434	0.056	0.17%	18.93°	0.115	1.8782	0.10 0.805
101.1 - 110.9	104.9	2.748	2671.763	0.055	0.10%	18.43°	0.064	1.0668	0.09 0.450
111.0 - 120.8	115.9	2.309	3419.390	0.054	0.07%	17.97°	0.050	0.8370	0.08 0.347
121.0 - 130.7	125.9	1.294	3332.278	0.058	0.04%	17.69°	0.022	0.3772	0.06 0.152
131.0 - 140.9	135.4	0.804	2988.048	0.043	0.03%	17.11°	0.011	0.1814	0.05 0.073
141.0 - 144.1	142.9	0.612	3058.135	0.045	0.02%	16.43°	0.008	0.1567	0.05 0.057

File name: P010589A.BND; size: 77121bytes; written: 1-5-1989 4059 scans

Profile ended: 01-05-1989 13:50:41

Units are meters, PAR: $\mu\text{E}/\text{m}^2$, kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in $\text{nE}/\text{m}^2/\text{s}/\text{str}$ from chlorophyll, Producted production in nM carbon/ m^3/sec .

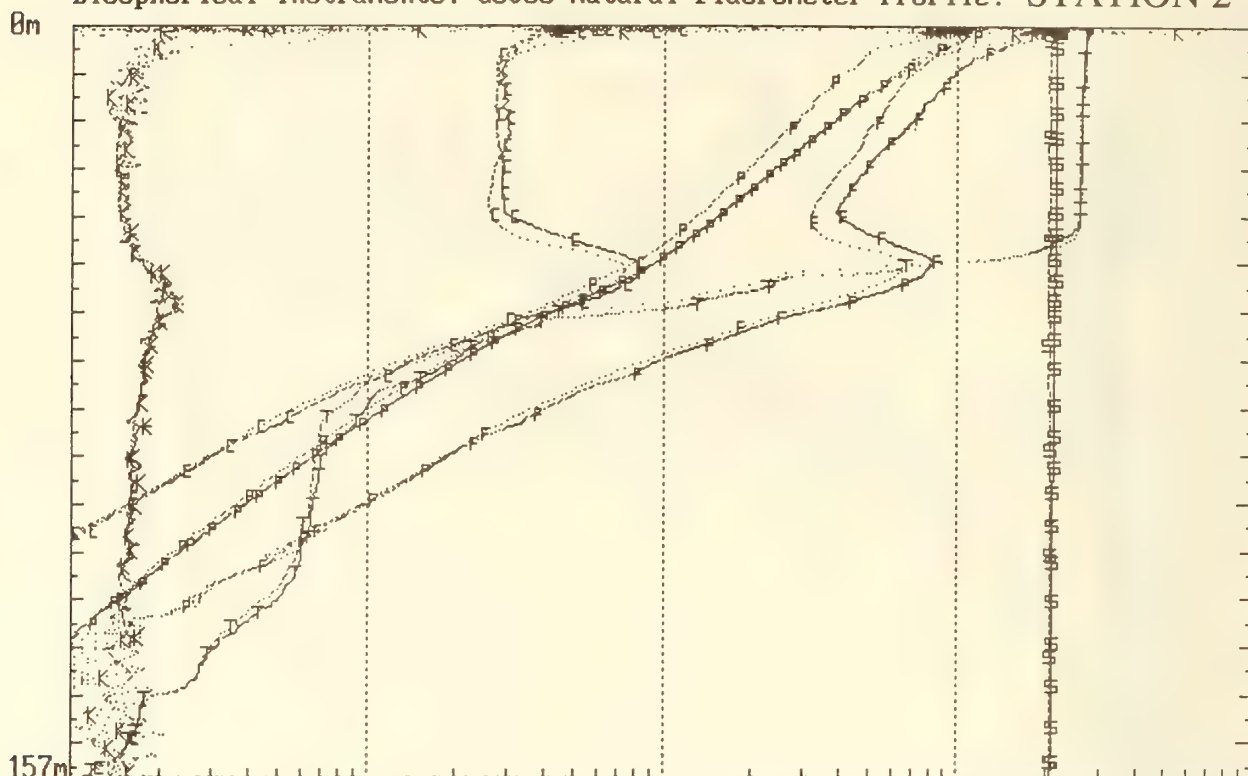
Chlorophyll (Chla) is in mg/m^3 assuming $\text{ac}(\text{PAR}) = .04$ and $\text{QE}(\text{F}) = .045$

Production assumes: $\text{a}(683) = .5$, $\text{QE}(\text{C/F}) = 2.4$; $\text{kcf} = 133$ 11.82378 to 14.0421

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 2



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.7	1026.546	2182.180	n.a.	n.a.	28.03°	20.512	0.1	
1.0 - 10.9	3.2	836.230	2173.130	0.188	38.48%	28.02°	16.222	47.0600	0.09 144.413
11.0 - 21.0	16.3	430.821	2140.507	0.046	20.13%	27.97°	7.470	29.5669	0.07 51.301
21.1 - 30.8	26.0	278.548	2137.270	0.044	13.03%	27.96°	5.454	29.1526	0.07 37.304
31.0 - 40.9	36.1	179.460	2135.271	0.044	8.40%	27.95°	4.105	28.9784	0.09 28.075
41.1 - 50.8	45.9	113.124	2131.371	0.052	5.31%	27.39°	5.999	55.3259	0.22 41.690
51.0 - 61.0	56.1	58.615	2127.869	0.079	2.75%	23.78°	5.179	61.9641	0.35 37.578
61.1 - 71.0	65.9	27.312	2116.637	0.067	1.29%	20.96°	1.559	22.6447	0.22 11.141
71.1 - 80.8	75.7	14.585	2107.659	0.060	0.69%	19.76°	0.590	9.2921	0.16 4.156
81.1 - 90.9	85.8	8.204	2107.809	0.054	0.39%	19.15°	0.262	4.2317	0.12 1.826
91.0 - 100.9	95.9	4.798	2099.092	0.053	0.23%	18.89°	0.131	2.1542	0.10 0.911
101.1 - 110.9	106.1	2.834	2091.835	0.050	0.14%	18.78°	0.067	1.1139	0.09 0.462
111.2 - 120.8	115.9	1.750	2082.688	0.047	0.08%	18.56°	0.035	0.5841	0.08 0.240
121.0 - 130.8	126.0	1.101	2078.253	0.043	0.05%	17.96°	0.016	0.2734	0.06 0.111
131.0 - 140.9	135.3	0.733	2076.214	0.041	0.04%	17.44°	0.010	0.1612	0.05 0.065
142.5 - 146.5	144.5	0.491	2078.287	0.033	0.02%	16.82°	0.008	0.1341	0.06 0.052

File name: P010689A.BND; size: 33440bytes; written: 1-6-1989 1760 scans

Profile ended: 01-06-1989 13:20:40

Units are meters, PAR: $\mu\text{E}/\text{m}^2$, kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in $\text{nE}/\text{m}^2/\text{s}/\text{str}$ from chlorophyll, Produced production in nM carbon/ m^3/sec .

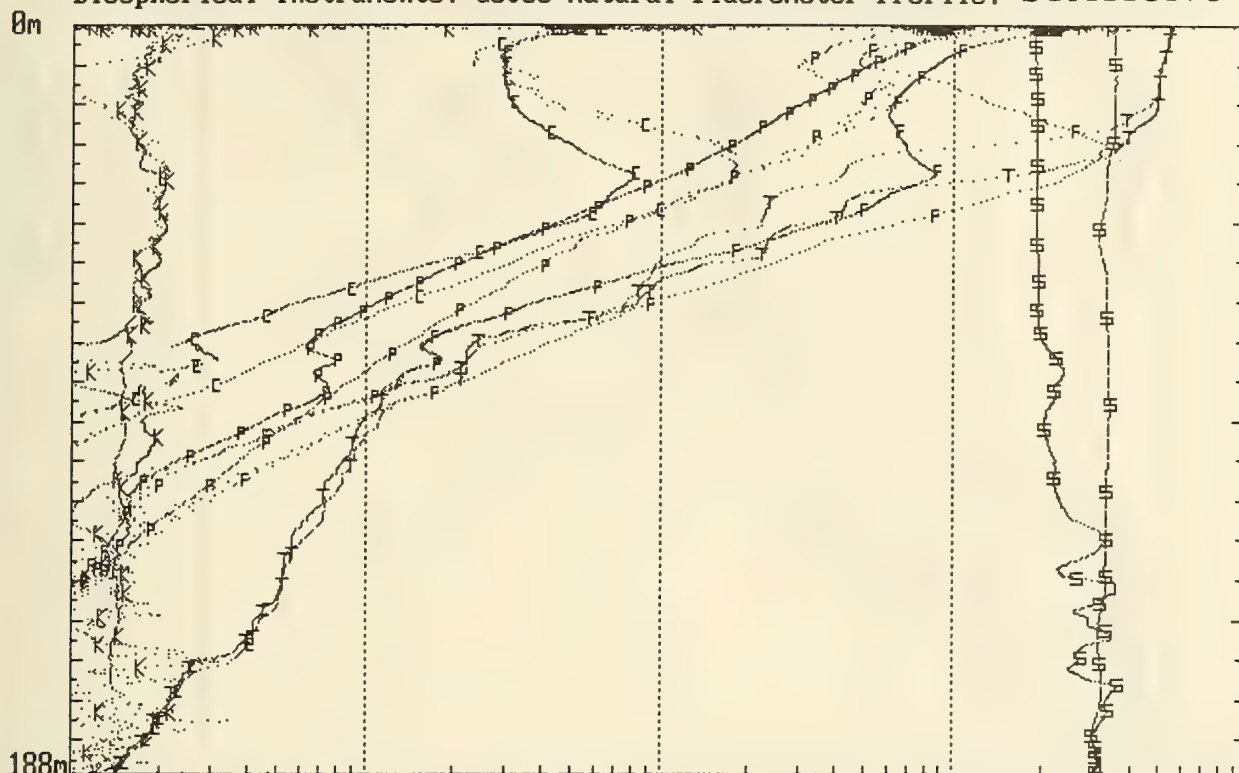
Chlorophyll (Chla) is in mg/m^3 assuming $a(\text{PAR}) = .04$ and $QE(F) = .045$

Production assumes: $a(683) = .5$, $QE(C/F) = 2.4$; $kcf = 133$ 12.38655 to 12.40841

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 3



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.7	930.331	2004.287	n.a.	n.a.	27.94°	22.147	0.1	
1.0 - 10.9	4.3	720.475	2164.394	0.133	33.29%	27.90°	14.752	42.3478	0.09 118.244
11.1 - 21.0	16.4	395.811	2064.289	0.050	19.17%	27.77°	7.575	31.8922	0.07 52.116
21.1 - 30.8	25.8	286.178	2392.450	0.052	11.96%	27.30°	11.726	58.5739	0.15 81.547
31.2 - 40.9	36.0	158.273	2383.796	0.068	6.64%	25.37°	14.049	104.0279	0.33 100.663
41.1 - 50.8	45.9	75.460	2333.917	0.075	3.23%	23.21°	6.962	75.7081	0.36 50.194
51.2 - 61.0	56.2	35.066	2280.779	0.071	1.54%	22.04°	2.397	33.0530	0.27 17.181
61.1 - 71.0	66.3	18.130	2303.674	0.061	0.79%	20.87°	0.821	12.3897	0.17 5.767
71.1 - 81.0	76.1	9.827	2247.822	0.049	0.44%	19.43°	0.305	4.7956	0.11 2.110
81.3 - 90.5	86.0	9.012	2836.997	0.044	0.32%	18.34°	0.225	3.5892	0.09 1.541
91.0 - 100.9	95.8	6.336	2526.248	0.052	0.25%	17.28°	0.102	1.6689	0.06 0.704
101.1 - 110.7	105.8	3.556	2541.511	0.058	0.14%	16.86°	0.048	0.8113	0.05 0.334
111.0 - 120.8	115.8	2.227	2647.209	0.035	0.08%	16.56°	0.025	0.4155	0.04 0.169
121.2 - 130.7	126.2	1.756	3124.148	0.028	0.06%	16.23°	0.018	0.2874	0.04 0.117
131.2 - 140.9	136.9	1.227	2862.739	0.038	0.04%	15.90°	0.012	0.1922	0.04 0.079
141.0 - 150.4	145.0	0.871	3223.935	0.042	0.03%	15.75°	0.009	0.1501	0.04 0.061
151.7 - 158.4	154.7	0.605	3062.411	0.032	0.02%	15.38°	0.008	0.1315	0.05 0.051
186.1 - 187.9	187.2	0.218	3209.096	0.024	0.01%	13.66°	0.010	0.1758	0.16 0.064

File name: P0107891.BND; size: 32946bytes; written: 1-7-1989 1734 scans

Profile ended: 01-07-1989 14:32:12

Units are meters, PAR: $\mu\text{E}/\text{m}^2$, kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in $\text{nE}/\text{m}^2/\text{s}/\text{str}$ from chlorophyll, Produced production in nM carbon/ m^3/sec .

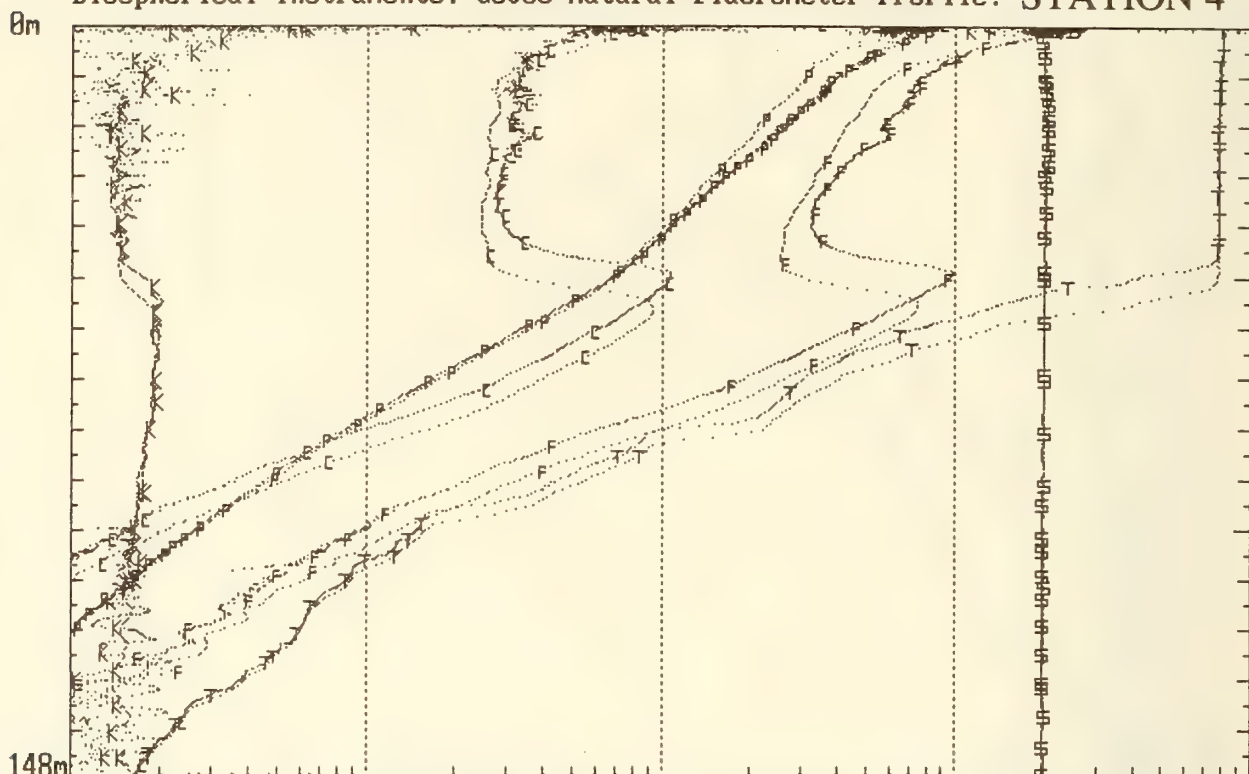
Chlorophyll (Chla) is in mg/m^3 cubed assuming $\text{ac}(\text{PAR}) = .04$ and $\text{QE}(\text{F}) = .045$

Production assumes: $\text{a}(683) = .5$, $\text{QE}(\text{C/F}) = 2.4$; $\text{kcf} = 133$ 12.44119 to 13.35366

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 4



<.01	.1 F:Natural Fluor	1	10 nE/m²/str/s	100>					
<1 S:Surf PAR	10 P: UW PAR	100 k:kpar(0-1)	1k µE/m²/sec	10k>					
<.1	1 C:Production	10	100 nMaC/m3/s	1k >					
< 14°	T:Temperature	21°	Celsius	28°>					
Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.6	667.484	2075.421	n.a.	n.a.	27.68°	21.366	0.2	
1.0 - 11.0	5.0	533.630	2002.458	0.099	26.65%	27.66°	13.165	47.5628	0.10 101.351
11.1 - 21.0	16.0	304.856	2053.605	0.046	14.84%	27.63°	6.372	32.0578	0.08 43.769
21.1 - 30.8	25.9	196.641	2051.806	0.045	9.58%	27.63°	4.624	30.7328	0.09 31.684
31.2 - 40.9	35.8	127.733	2022.292	0.042	6.32%	27.63°	3.321	27.9875	0.10 22.624
41.1 - 50.8	45.4	85.291	2015.588	0.044	4.23%	27.49°	4.687	48.2790	0.22 32.198
51.0 - 61.0	56.2	46.968	2006.413	0.068	2.34%	25.36°	6.298	80.2706	0.54 44.998
61.3 - 70.8	65.9	23.478	2003.615	0.071	1.17%	23.45°	3.179	47.8441	0.54 22.831
71.1 - 81.0	75.9	11.645	1994.640	0.068	0.58%	22.23°	1.270	20.7566	0.42 9.077
81.5 - 90.9	86.1	5.977	1989.522	0.062	0.30%	20.46°	0.409	7.0765	0.26 2.891
91.0 - 100.9	97.0	3.133	1982.379	0.053	0.16%	18.65°	0.140	2.3845	0.17 0.975
101.1 - 110.9	105.6	1.979	1973.611	0.049	0.10%	17.63°	0.066	1.1024	0.13 0.458
111.0 - 120.8	115.8	1.221	1974.316	0.045	0.06%	16.88°	0.036	0.5940	0.11 0.245
121.0 - 130.8	125.8	0.779	1976.923	0.043	0.04%	16.33°	0.020	0.3379	0.10 0.139
131.0 - 140.9	135.8	0.519	1989.019	0.042	0.03%	15.47°	0.010	0.1720	0.07 0.070
141.0 - 147.8	143.0	0.386	1982.793	0.043	0.02%	15.01°	0.008	0.1371	0.07 0.051

File name: P013089A.BND; size: 34903bytes; written: 1-30-1989 1837 scans

Profile ended: 01-30-1989 13:44:48

Units are meters, PAR: μ E/m², kPAR:1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in nE/m²/s/str from chlorophyll, Produced production in nM carbon/m³/sec.

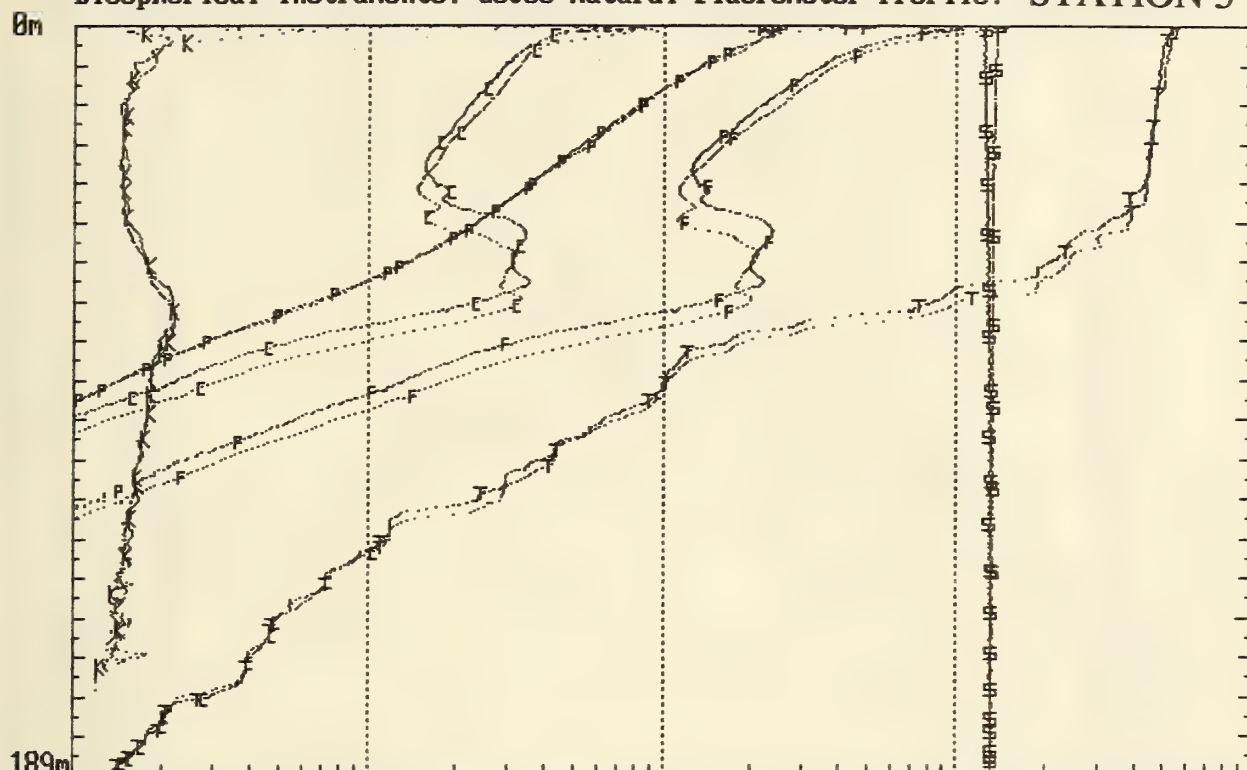
Chlorophyll (Chla) is in mg/m cubed assuming ac(PAR) = .04 and QE(F) = .045

Production assumes: a(683)= .5, QE(C/F)= 2.4; kcf= 133 12.58872 to 14.38086

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 5



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.4	398.114	1344.676	n.a.	n.a.	28.95°	12.768	0.2	
1.0 - 10.7	4.8	196.532	1275.898	0.105	15.40%	28.85°	6.318	47.4150	0.13 49.436
11.2 - 20.8	16.1	101.528	1289.615	0.048	7.87%	28.74°	2.793	27.0568	0.11 19.262
21.1 - 30.7	25.8	66.112	1292.656	0.042	5.11%	28.66°	1.850	20.7311	0.11 12.607
31.0 - 40.9	36.4	42.365	1289.742	0.042	3.28%	28.59°	1.324	16.7835	0.12 9.010
41.1 - 50.8	46.2	27.943	1296.647	0.044	2.16%	28.35°	1.471	20.3593	0.21 10.055
51.2 - 61.0	56.1	17.362	1297.091	0.056	1.34%	27.63°	2.067	31.1268	0.48 14.453
61.3 - 70.8	66.1	9.216	1300.388	0.074	0.71%	26.57°	1.886	31.1570	0.84 13.582
71.1 - 81.0	75.8	4.232	1301.514	0.082	0.33%	24.25°	0.849	15.0157	0.78 6.227
81.1 - 90.7	86.1	1.922	1305.703	0.069	0.15%	22.29°	0.230	4.2107	0.47 1.652
91.0 - 100.8	95.7	1.008	1305.578	0.064	0.08%	21.73°	0.097	1.7221	0.38 0.690
101.1 - 110.9	106.0	0.537	1306.365	0.058	0.04%	20.71°	0.040	0.6957	0.28 0.278
111.0 - 120.8	116.2	0.306	1307.110	0.053	0.02%	19.87°	0.018	0.3088	0.22 0.124
121.2 - 130.4	125.6	0.188	1306.075	0.048	0.01%	18.57°	0.009	0.1545	0.18 0.062

File name: P031189D.BND; size: 22002bytes; written: 3-11-1989 1158 scans

Profile ended: 03-11-1989 14:44:56

Units are meters, PAR: $\mu\text{E}/\text{m}^2$, kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (kPAR) in 1/meters, 15 point smooth.

Natural Fluorescence in $\text{nE}/\text{m}^2/\text{s}/\text{str}$ from chlorophyll, Producted production in nM carbon/ m^3/sec .

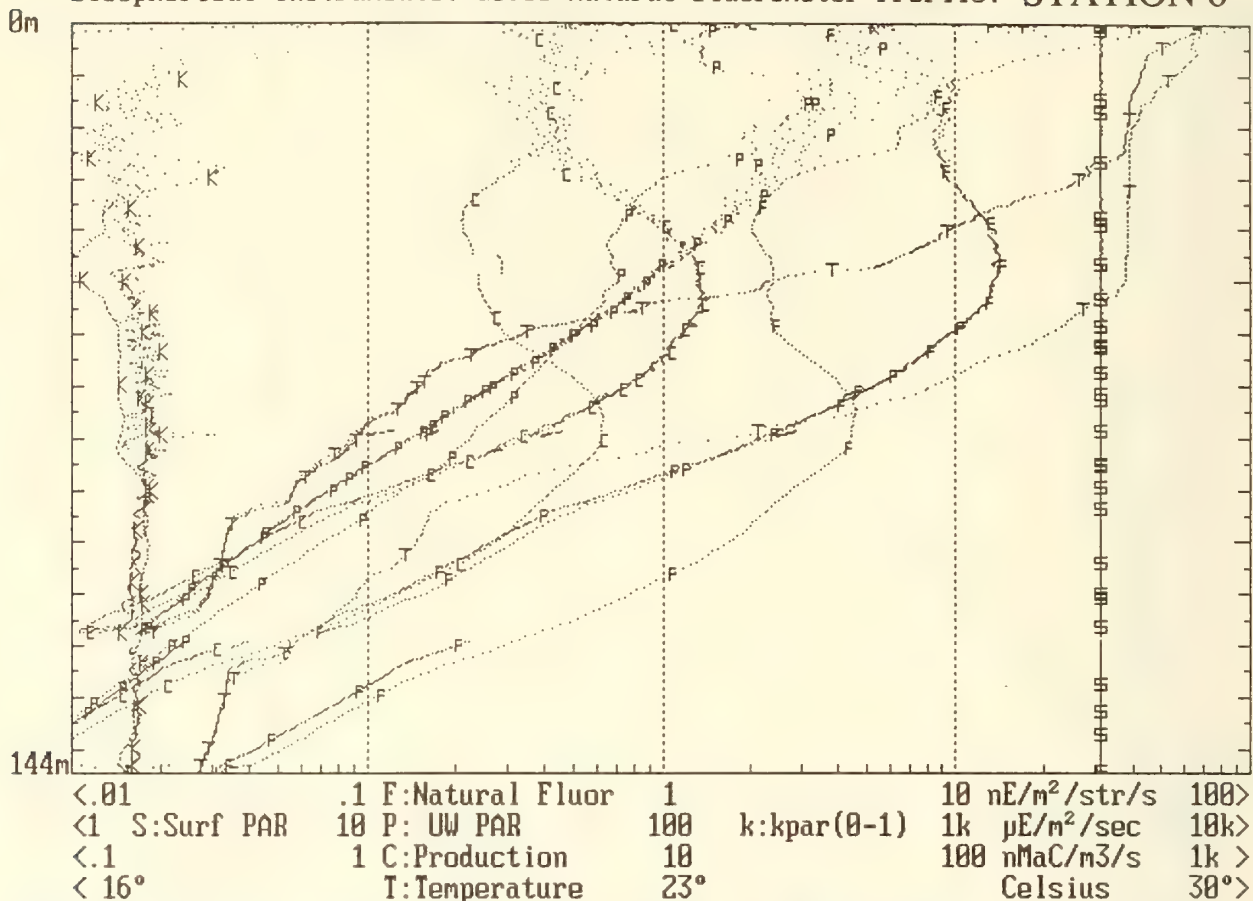
Chlorophyll (Chla) is in mg/m cubed assuming $\text{ac}(\text{PAR}) = .04$ and $\text{QE}(\text{F}) = .045$

Production assumes: $\text{a}(683) = .5$, $\text{QE}(\text{C}/\text{F}) = 2.4$; $\text{kcf} = 133$ 12.84005 to 12.89469

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 6



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.5	933.282	3130.141	n.a.	n.a.	29.39°	26.456	0.2	
1.1 - 10.9	6.0	402.165	3107.976	0.074	12.94%	29.24°	11.771	54.3035	0.13 87.670
11.1 - 21.0	16.2	370.650	3117.082	0.052	11.89%	28.65°	8.805	41.0808	0.10 61.025
21.3 - 30.8	26.2	233.427	3117.764	0.050	7.49%	28.38°	7.481	44.5464	0.12 50.891
31.2 - 40.9	36.2	147.629	3119.846	0.044	4.73%	27.46°	8.858	66.0017	0.21 60.791
41.1 - 50.7	46.0	102.804	3124.794	0.046	3.29%	25.96°	11.828	110.0987	0.43 82.020
51.0 - 61.0	56.4	62.168	3124.226	0.054	1.99%	23.35°	9.705	111.6094	0.61 67.957
61.1 - 71.0	66.0	35.870	3122.262	0.059	1.15%	21.63°	6.294	84.8371	0.70 44.342
71.1 - 81.0	76.2	19.515	3122.126	0.063	0.63%	20.38°	3.437	51.1650	0.69 24.246
81.1 - 90.9	85.6	11.389	3120.451	0.061	0.36%	19.50°	1.703	26.6828	0.55 11.953
91.2 - 100.8	95.8	6.184	3118.745	0.059	0.20%	18.54°	0.765	12.5783	0.42 5.393
101.1 - 110.9	106.0	3.482	3118.532	0.055	0.11%	18.14°	0.394	6.5971	0.38 2.764
111.0 - 120.7	115.5	2.104	3118.475	0.050	0.07%	17.62°	0.175	2.9592	0.28 1.219
121.0 - 130.7	125.7	1.675	3110.435	0.055	0.05%	18.01°	0.131	2.2154	0.30 0.915
131.0 - 140.7	135.9	0.958	3109.275	0.054	0.03%	17.70°	0.061	1.0455	0.24 0.424
141.0 - 144.6	143.0	0.656	3106.360	0.047	0.02%	17.54°	0.035	0.5966	0.20 0.240

File name: P031389B.BND; size: 22287bytes; written: 3-13-1989 1173 scans

Profile began: 03-13-1989 13:01:52 - Profile ended: 03-13-1989 13:06:58

Units are meters, PAR: µE/m², kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in nE/m²/s/str from chlorophyll, Produced production in nM carbon/m³/sec.

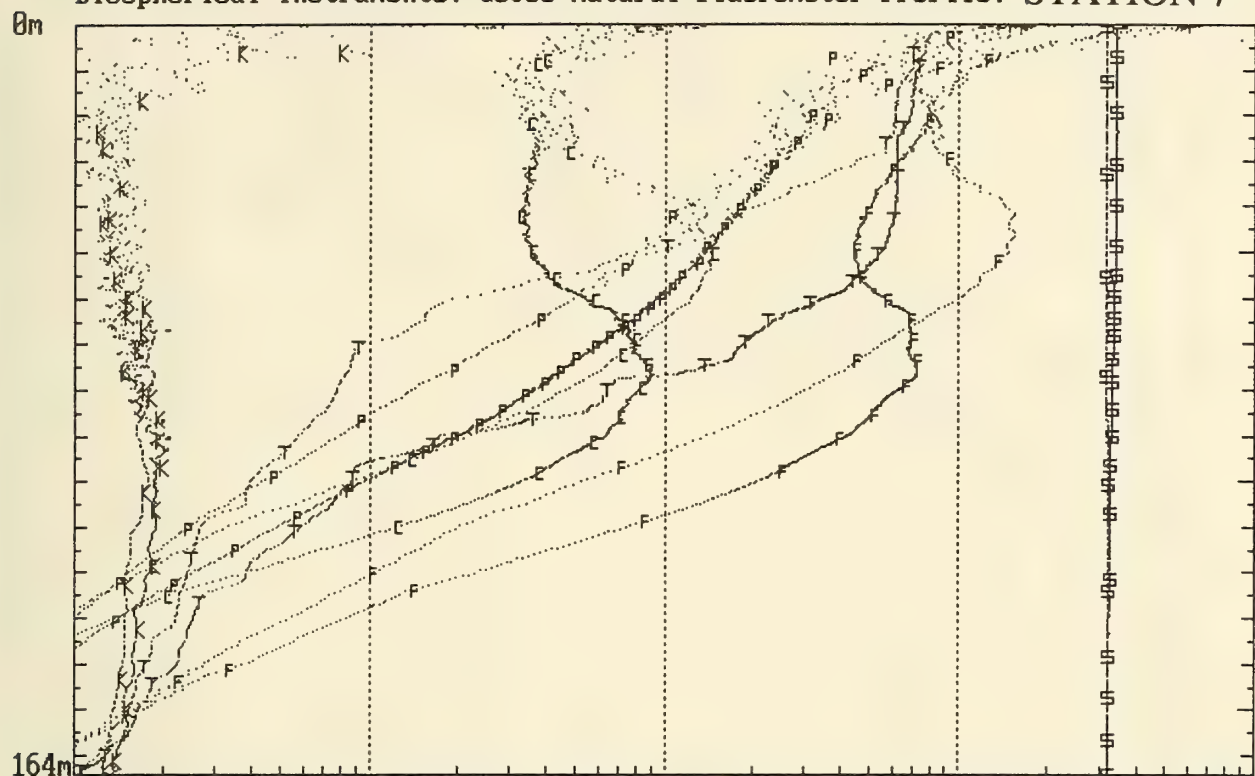
Chlorophyll (Chla) is in mg/m cubed assuming ac(PAR) = .04 and QE(F) = .045

Production assumes: a(683)= .5, QE(C/F)= 2.4; kcf= 133 12.69253 to 12.73624

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 7



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.5	1618.456	3148.153	n.a.	n.a.	29.90°	57.704	0.2	
1.2 - 10.7	5.8	809.040	3320.599	0.115	24.36%	29.79°	20.163	53.8419	0.11 157.487
11.0 - 20.8	16.0	371.880	3313.767	0.047	11.22%	28.72°	8.391	38.2771	0.09 57.524
21.1 - 30.8	26.0	264.874	3328.661	0.031	7.96%	28.52°	7.669	42.2634	0.11 51.171
31.0 - 40.8	35.9	194.629	3341.720	0.032	5.82%	28.11°	7.395	51.0544	0.15 49.787
41.1 - 50.8	46.0	140.248	3341.513	0.034	4.20%	27.66°	7.345	62.5534	0.23 49.654
51.0 - 61.0	56.4	100.501	3341.594	0.041	3.01%	26.96°	6.243	61.8698	0.28 42.686
61.3 - 71.0	65.9	67.127	3321.938	0.049	2.02%	25.70°	6.796	76.1134	0.43 46.876
71.1 - 81.0	76.0	39.372	3289.992	0.053	1.20%	24.13°	6.290	80.8991	0.65 43.613
81.1 - 90.9	86.2	22.465	3269.089	0.062	0.69%	22.34°	4.325	62.9590	0.77 30.548
91.0 - 100.8	95.5	11.518	3245.874	0.068	0.35%	20.30°	2.367	37.9301	0.78 16.949
101.1 - 110.7	105.7	5.455	3229.855	0.065	0.17%	19.33°	0.936	16.0057	0.62 6.668
111.0 - 120.8	115.8	2.761	3220.513	0.058	0.09%	18.48°	0.293	5.2057	0.38 2.067
121.0 - 130.7	125.8	1.551	3216.714	0.051	0.05%	17.87°	0.102	1.8061	0.25 0.710
131.0 - 140.4	135.7	0.932	3211.577	0.047	0.03%	17.47°	0.046	0.7981	0.18 0.315
141.0 - 150.4	145.7	0.587	3209.418	0.042	0.02%	17.07°	0.022	0.3794	0.14 0.150
151.1 - 160.8	156.2	0.393	3209.776	0.037	0.01%	16.65°	0.011	0.1851	0.10 0.074
161.2 - 162.0	161.6	0.326	3208.709	0.030	0.01%	16.31°	0.007	0.1604	0.08 0.048

File name: P031389C.BND; size: 20957bytes; written: 3-13-1989 1103 scans

Profile ended: 03-13-1989 13:28:40

Units are meters, PAR: $\mu\text{E}/\text{m}^2$, kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in $\text{nE}/\text{m}^2/\text{s}/\text{str}$ from chlorophyll, Producted production in nM carbon/ m^3/sec .

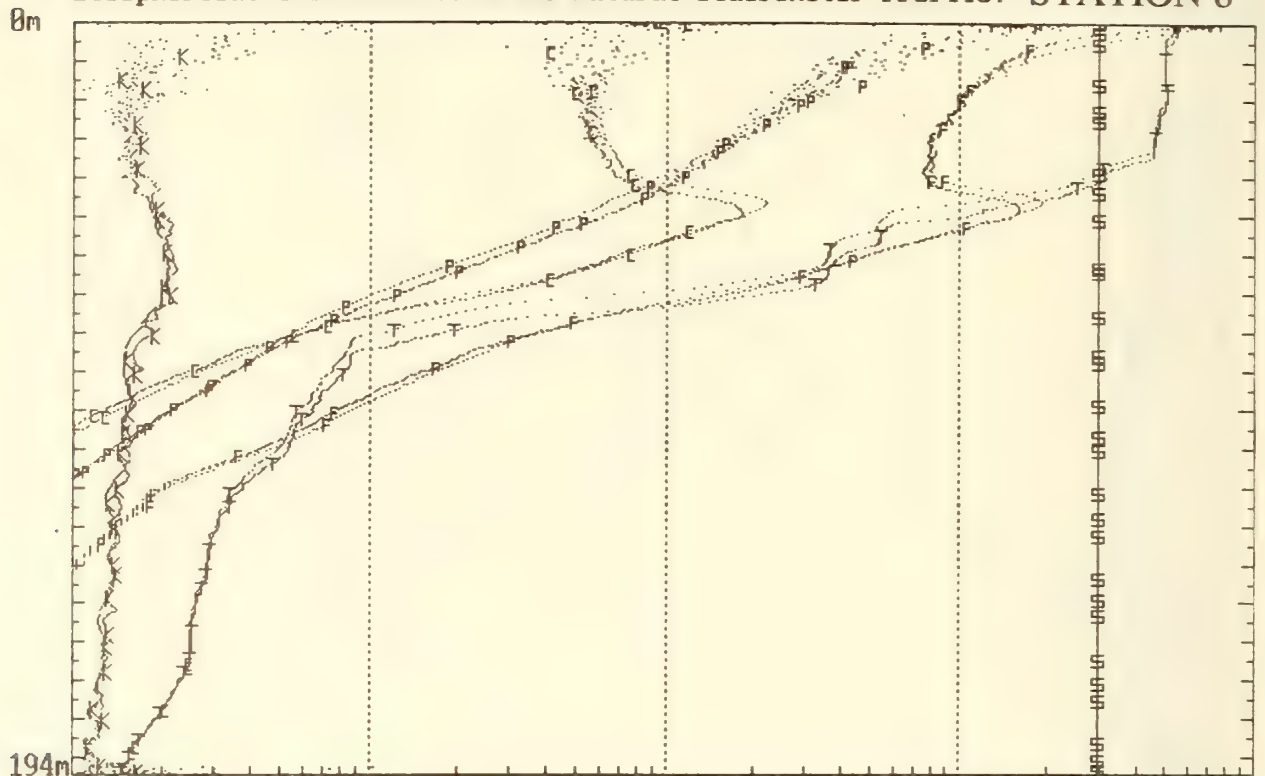
Chlorophyll (Chla) is in mg/m^3 assuming $a(\text{PAR}) = .04$ and $QE(F) = .045$

Production assumes: $a(683) = .5$, $QE(C/F) = 2.4$; $kcf = 133$ 12.16254 to 12.74717

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 8



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.5	1582.751	2982.856	n.a.	n.a.	28.92°	63.572	0.2	
1.2 - 10.8	6.2	806.032	2984.323	0.119	27.01%	28.83°	23.925	69.0948	0.14 190.987
11.1 - 21.0	16.2	350.249	2985.508	0.054	11.73%	28.80°	11.520	54.7150	0.13 80.260
21.1 - 30.7	25.9	213.668	2986.039	0.045	7.16%	28.70°	8.899	57.3986	0.16 60.959
31.0 - 40.9	36.0	132.341	2986.735	0.050	4.43%	28.27°	7.937	67.5399	0.24 54.819
41.2 - 50.8	46.0	76.628	2987.960	0.064	2.56%	26.65°	13.732	152.9199	0.77 97.593
51.2 - 60.8	55.9	37.393	2986.688	0.079	1.25%	24.73°	7.913	109.5272	0.85 57.511
61.1 - 71.0	65.9	16.872	2986.854	0.080	0.56%	23.68°	2.792	45.0753	0.66 20.353
71.1 - 81.0	76.1	7.774	2986.354	0.068	0.26%	20.03°	0.668	11.6751	0.33 4.788
81.1 - 90.7	86.0	4.345	2984.579	0.051	0.15%	17.87°	0.226	3.8526	0.20 1.565
91.0 - 100.8	96.1	2.657	2983.748	0.048	0.09%	17.33°	0.108	1.8192	0.15 0.743
101.1 - 110.7	106.0	1.676	2983.255	0.044	0.06%	16.96°	0.059	0.9846	0.13 0.401
111.0 - 120.8	116.1	1.076	2983.027	0.041	0.04%	16.49°	0.028	0.4697	0.10 0.190
121.2 - 130.8	126.1	0.738	2982.570	0.035	0.02%	16.04°	0.016	0.2710	0.08 0.110
131.0 - 140.9	136.0	0.522	2983.341	0.034	0.02%	15.85°	0.012	0.1953	0.09 0.080
141.0 - 150.9	145.9	0.373	2982.925	0.032	0.01%	15.74°	0.009	0.1424	0.09 0.058
151.1 - 160.2	154.7	0.277	2982.500	0.029	0.01%	15.62°	0.007	0.1202	0.10 0.048

File name: P031889A.BND; size: 23085bytes; written: 3-18-1989 1215 scans

Profile ended: 03-18-1989 10:19:01

Units are meters, PAR: $\mu\text{E}/\text{m}^2$, kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in $\text{nE}/\text{m}^2/\text{s}/\text{str}$ from chlorophyll, Producted production in nM carbon/ m^3/sec .

Chlorophyll (Chla) is in mg/m^3 assuming $a(\text{PAR}) = .04$ and $Q\text{E}(\text{F}) = .045$

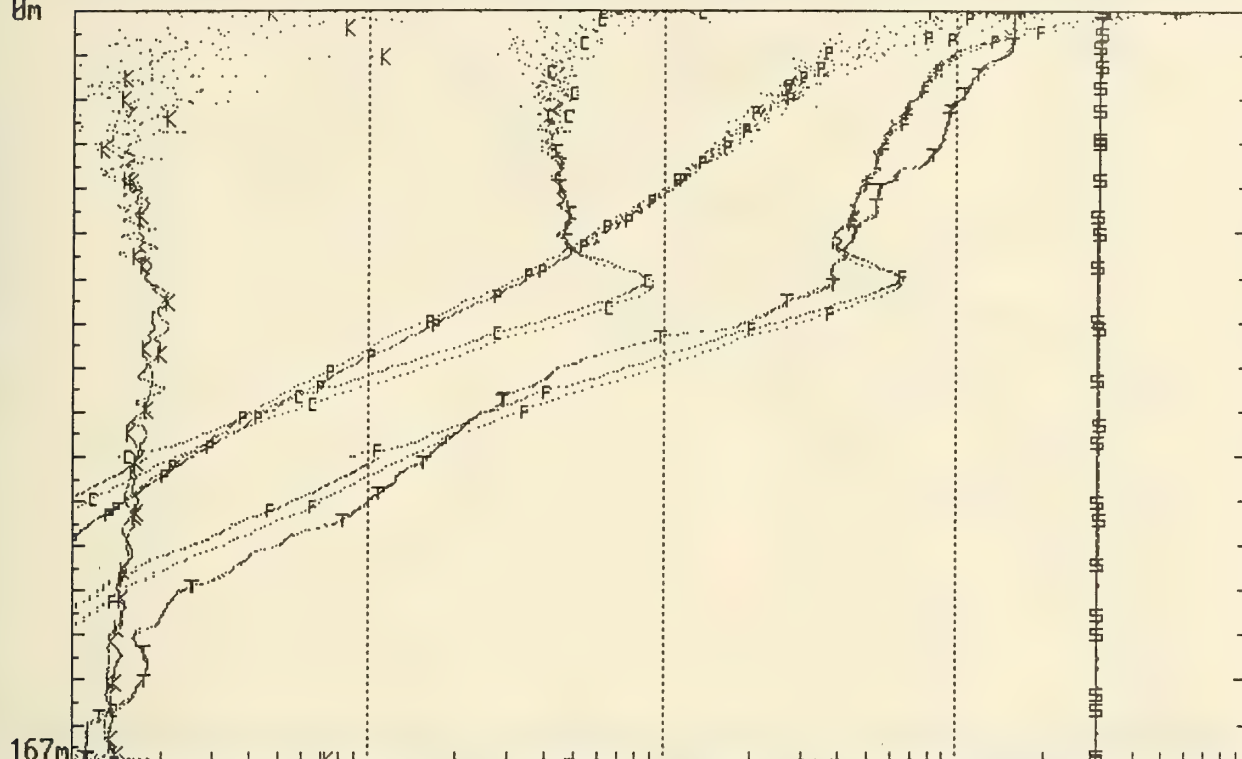
Production assumes: $a(683) = .5$, $Q\text{E}(\text{C}/\text{F}) = 2.4$; $k\text{cf} = 133$ 12.64882 to 12.6816

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 9

0m



167m

<.01 1 F:Natural Fluor 1 10 nE/m²/str/s 100>
 <1 S:Surf PAR 10 P: UW PAR 100 k:kpar(0-1) 1k μ E/m²/sec 10k>
 <.1 1 C:Production 10 100 nMaC/m³/s 1k>
 < 15° T:Temperature 24° Celsius 33°>

Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.3	1569.639	3127.215	n.a.	n.a.	29.45°	55.959	0.2	
1.1 - 10.9	6.5	685.854	3099.008	0.126	22.13%	29.33°	15.604	50.5061	0.11 125.423
11.0 - 21.0	16.2	301.826	3074.815	0.067	9.82%	28.73°	7.989	42.6975	0.11 56.847
21.1 - 30.7	25.6	198.273	3060.529	0.050	6.48%	28.34°	6.251	42.3509	0.12 43.209
31.0 - 40.8	35.8	126.940	3051.315	0.045	4.16%	27.78°	5.193	44.3309	0.16 35.561
41.1 - 50.7	45.8	77.191	3042.464	0.053	2.54%	27.17°	4.396	47.1476	0.22 30.541
51.0 - 61.0	55.8	44.365	3037.666	0.059	1.46%	26.75°	4.911	63.6523	0.46 34.543
61.3 - 70.8	65.8	22.865	3037.139	0.073	0.75%	25.90°	4.314	64.3650	0.75 31.076
71.1 - 80.8	75.9	11.093	3037.164	0.067	0.37%	23.43°	1.371	22.9659	0.48 9.789
81.1 - 90.7	85.9	5.736	3036.736	0.064	0.19%	21.76°	0.457	7.9483	0.31 3.244
91.0 - 100.8	95.8	3.209	3036.548	0.055	0.11%	20.77°	0.176	3.0317	0.21 1.226
101.1 - 110.9	105.9	1.856	3036.027	0.051	0.06%	19.86°	0.083	1.4177	0.17 0.573
111.2 - 120.8	115.9	1.122	3035.437	0.049	0.04%	18.74°	0.039	0.6766	0.13 0.272
121.0 - 130.8	125.9	0.703	3034.518	0.044	0.02%	17.30°	0.018	0.3065	0.10 0.122
131.0 - 140.9	136.0	0.463	3033.459	0.040	0.02%	16.30°	0.010	0.1725	0.08 0.069
141.0 - 150.8	145.7	0.325	3033.198	0.035	0.01%	16.08°	0.008	0.1322	0.09 0.054
151.2 - 152.4	151.8	0.269	3038.298	0.032	0.01%	16.01°	0.007	0.1585	0.10 0.048

File name: P032189A.BND; size: 21014bytes; written. 3-21-1989 1106 scans

Profile ended: 03-21-1989 08:12:27

Units are meters, PAR: μ E/m², kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in nE/m²/s/str from chlorophyll, Producted production in nM carbon/m³/sec.

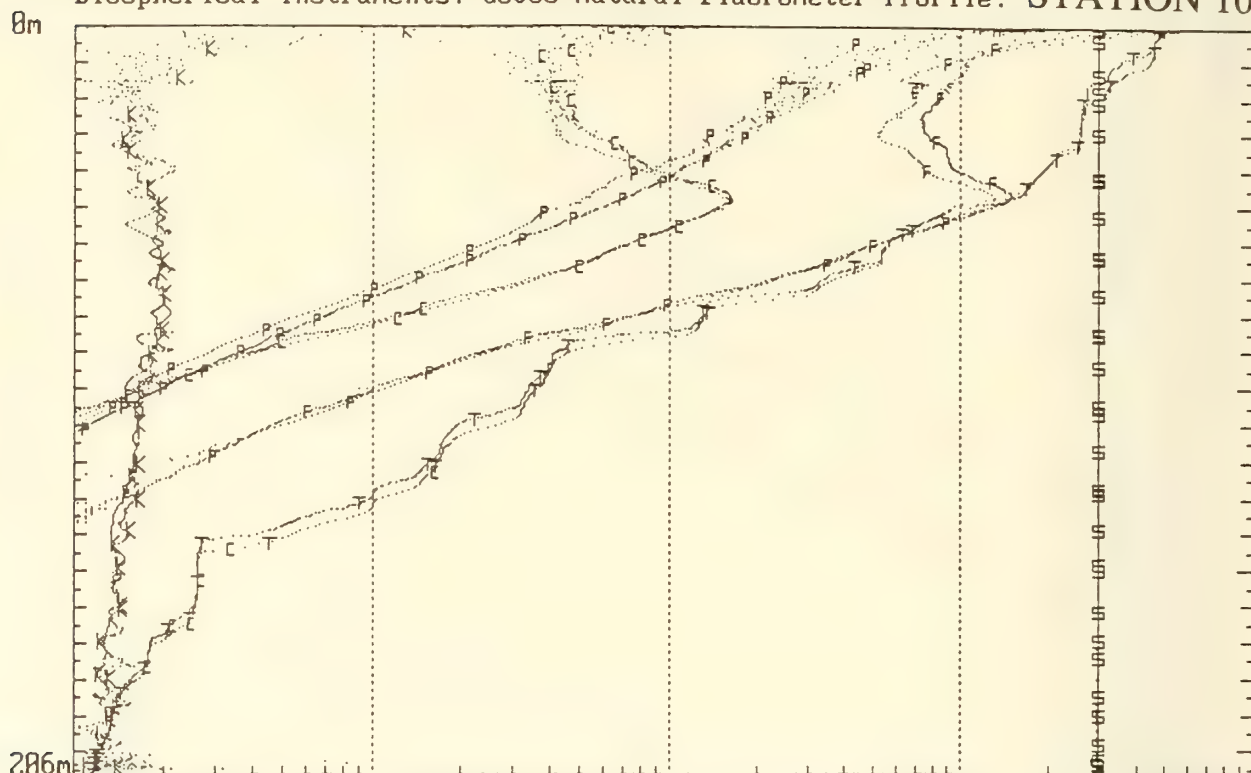
Chlorophyll (Chla) is in mg/m cubed assuming ac(PAR) = .04 and QE(F) = .045

Production assumes: a(683) = .5, QE(C/F) = 2.4; kcf = 133 12.08604 to 12.6816

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 10



<.01 .1 F:Natural Fluor 1 10 nE/m²/str/s 100>
 <1 S:Surf PAR 10 P: UW PAR 100 k:kpar(0-1) 1k µE/m²/sec 10k>
 <.1 1 C:Production 10 100 nMaC/m³/s 1k >
 < 13° T:Temperature 22° Celsius 31°>

Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.4	1564.690	2989.122	n.a.	n.a.	29.61°	48.209	0.2	
1.1 - 10.9	5.9	679.092	2977.701	0.110	22.81%	29.38°	15.864	52.2605	0.11 125.591
11.0 - 21.0	16.2	313.451	2972.684	0.050	10.54%	28.69°	8.101	41.2062	0.10 56.019
21.1 - 30.8	25.9	203.874	2975.744	0.050	6.85%	28.37°	6.985	46.6297	0.13 48.289
31.2 - 40.9	36.0	124.881	2975.348	0.053	4.20%	28.02°	8.259	72.5023	0.26 57.368
41.1 - 50.8	46.0	70.407	2973.711	0.062	2.37%	27.23°	12.489	140.3651	0.73 88.155
51.2 - 60.8	56.0	36.564	2971.820	0.068	1.23%	25.75°	7.594	103.6217	0.82 54.149
61.1 - 71.0	65.9	18.259	2969.881	0.071	0.61%	24.95°	3.277	51.2705	0.71 23.513
71.1 - 81.0	76.1	8.839	2968.185	0.072	0.30%	23.17°	1.184	20.0279	0.53 8.512
81.1 - 90.9	86.3	4.324	2967.267	0.068	0.15%	21.28°	0.375	6.5130	0.34 2.676
91.2 - 100.9	96.2	2.315	2964.390	0.057	0.08%	20.10°	0.145	2.5136	0.24 1.018
101.3 - 110.9	106.2	1.336	2962.546	0.053	0.05%	19.47°	0.065	1.1236	0.19 0.454
111.2 - 120.7	116.0	0.793	2960.899	0.051	0.03%	18.57°	0.032	0.5549	0.16 0.223
121.0 - 130.8	126.3	0.480	2959.870	0.047	0.02%	17.87°	0.017	0.2976	0.14 0.120
131.0 - 140.9	136.1	0.312	2958.681	0.040	0.01%	16.54°	0.010	0.1643	0.12 0.066
141.2 - 145.2	143.0	0.236	2961.014	0.038	0.01%	14.94°	0.007	0.1320	0.12 0.049

File name: P032289A.BND; size: 25346bytes; written: 3-22-1989 1334 scans

Profile ended: 03-22-1989 08:09:13

Units are meters, PAR: µE/m², kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in nE/m²/s/str from chlorophyll, Produced production in nM carbon/m³/sec.

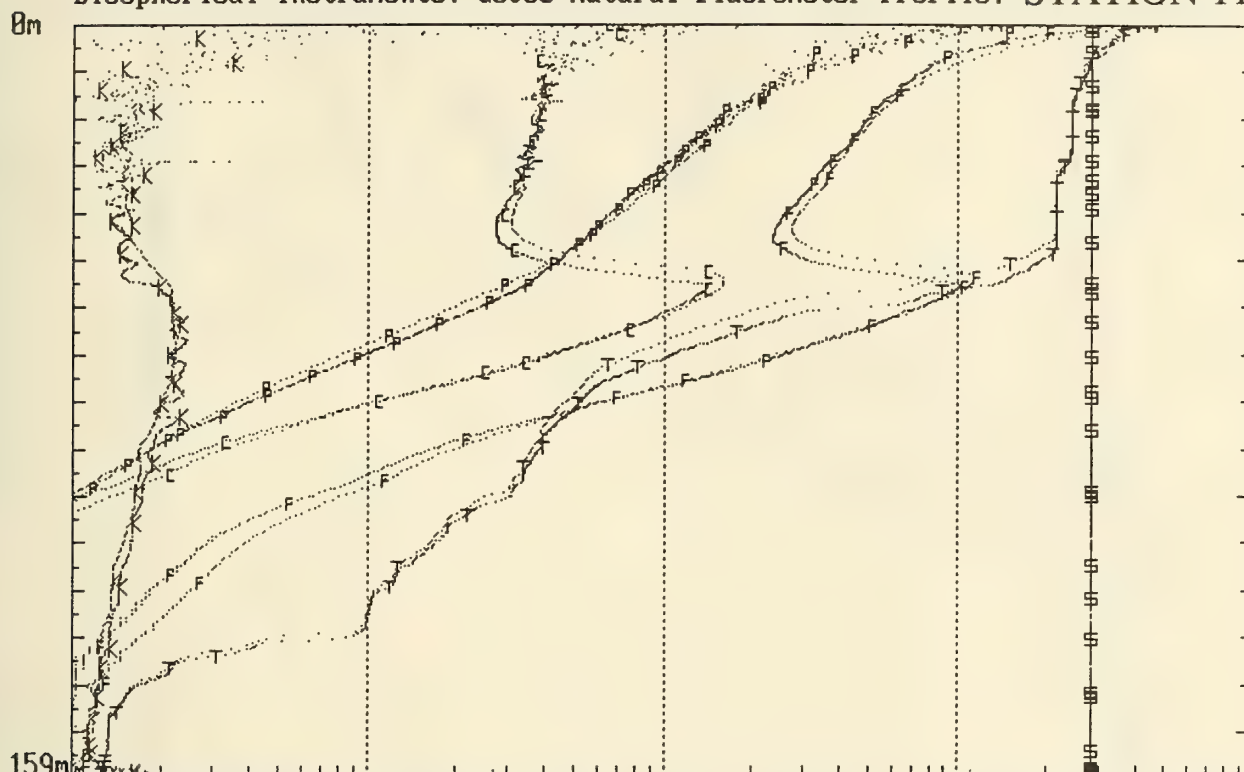
Chlorophyll (Chla) is in mg/m cubed assuming ac(PAR) = .04 and QE(F) = .045

Production assumes: a(683)= .5, QE(C/F)= 2.4; kcf= 133 12.65975 to 12.69253

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 11



<.01		.1 F:Natural Fluor		1		10 nE/m ² /str/s		100>	
<1 S:Surf PAR		10 P: UW PAR		100		k:kpar(0-1)		1k uE/m ² /sec	
<.1		1 C:Production		10		100 nMaC/m ³ /s		1k >	
< 14°		T:Temperature		23°		Celsius		32°>	
Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.5	1042.735	2838.193	n.a.	n.a.	30.07°	37.083	0.2	
1.1 - 11.0	5.4	527.887	2836.772	0.135	18.61%	29.72°	14.300	56.6879	0.12 117.987
11.0 - 21.0	16.1	205.045	2836.485	0.055	7.23%	29.30°	5.900	39.4603	0.11 41.184
21.1 - 30.8	26.0	124.285	2837.037	0.046	4.38%	29.22°	4.214	36.1870	0.13 28.910
31.0 - 40.9	35.6	81.340	2839.150	0.041	2.86%	29.01°	3.119	31.9203	0.15 21.227
41.1 - 50.8	45.9	53.318	2840.452	0.045	1.88%	28.92°	2.806	33.6703	0.21 19.255
51.0 - 60.8	55.9	31.316	2840.878	0.070	1.10%	27.14°	8.340	117.4631	1.13 59.939
61.1 - 71.0	66.2	13.524	2839.067	0.088	0.48%	23.75°	4.092	67.0726	1.23 30.248
71.1 - 81.0	75.9	5.707	2835.008	0.086	0.20%	22.09°	1.223	21.6486	0.85 9.023
81.1 - 90.9	85.7	2.573	2835.738	0.072	0.09%	21.30°	0.315	5.6955	0.48 2.269
91.2 - 100.8	95.9	1.307	2836.094	0.060	0.05%	20.81°	0.108	1.9239	0.32 0.759
101.3 - 110.9	106.1	0.743	2837.309	0.050	0.03%	19.80°	0.044	0.7634	0.22 0.302
111.2 - 120.7	115.9	0.474	2835.240	0.040	0.02%	19.00°	0.025	0.4293	0.20 0.172
121.0 - 130.8	126.0	0.329	2835.227	0.033	0.01%	18.32°	0.017	0.2850	0.19 0.115
131.2 - 140.9	136.2	0.243	2834.226	0.024	0.01%	15.69°	0.012	0.1908	0.18 0.077
141.2 - 150.8	146.0	0.199	2830.856	0.018	0.01%	14.67°	0.010	0.1663	0.19 0.068
151.1 - 159.0	156.9	0.178	2832.119	0.071	0.01%	14.49°	0.010	0.1687	0.22 0.070

File name: P0322898.BND; size: 23674bytes; written: 3-22-1989 1246 scans

Profile ended: 03-22-1989 14:35:33

Units are meters, PAR: uE/m², kPAR:1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in nE/m²/s/str from chlorophyll, Produced production in nM carbon/m³/sec.

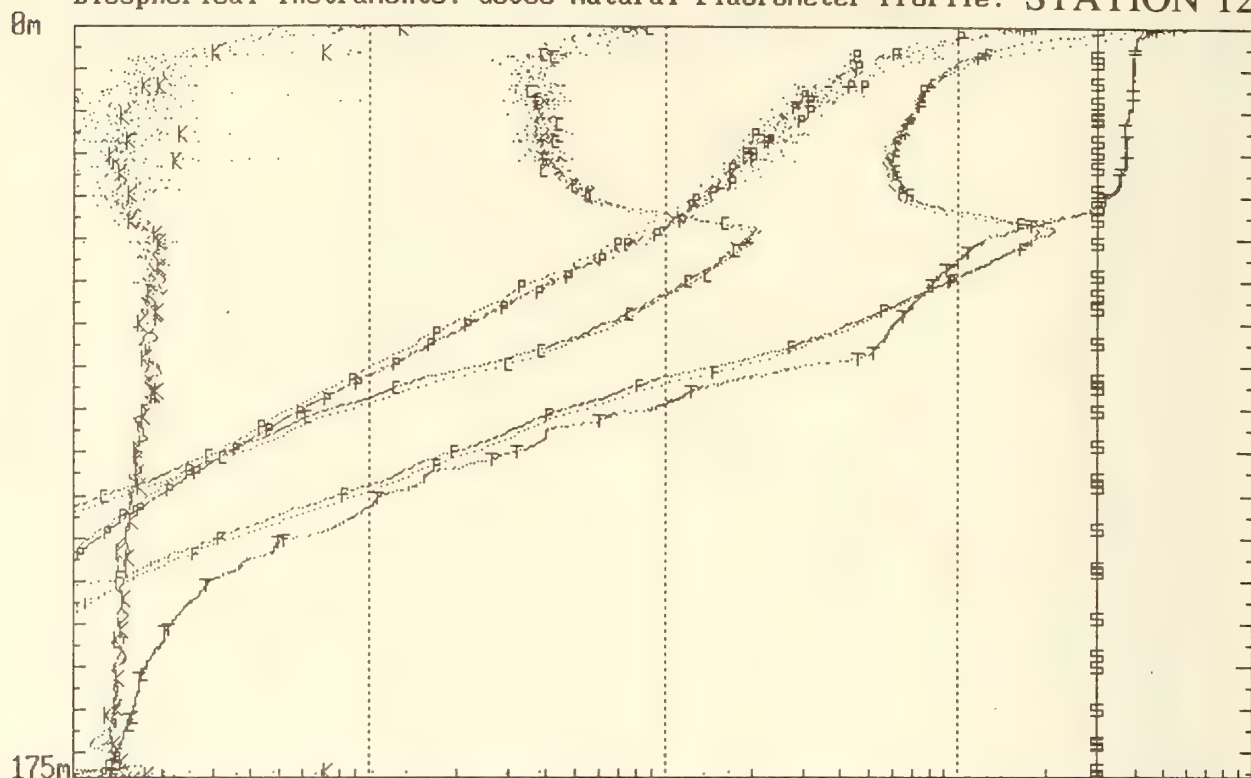
Chlorophyll (Chla) is in mg/m cubed assuming ac(PAR) = .04 and QE(F) = .045

Production assumes: a(683)= .5, QE(C/F)= 2.4; kcf= 133 12.64336 to 12.67067

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 12



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.5	1610.624	2982.885	n.a.	n.a.	29.39°	47.333	0.2	
1.1 - 10.9	6.4	699.471	2984.151	0.121	23.44%	29.21°	15.276	45.6426	0.09 122.376
11.1 - 21.0	16.1	341.044	2985.363	0.060	11.42%	29.16°	7.666	37.0861	0.09 53.953
21.1 - 30.5	26.0	233.115	2986.180	0.045	7.81%	29.07°	6.366	38.5570	0.11 43.618
31.0 - 40.8	35.2	168.374	2986.773	0.049	5.64%	28.97°	6.212	46.2120	0.15 42.840
41.1 - 50.8	45.8	105.354	2986.986	0.053	3.53%	27.83°	14.151	136.2560	0.56 98.787
51.0 - 61.0	55.7	56.286	2987.121	0.067	1.88%	26.44°	12.743	153.3419	0.90 90.834
61.3 - 71.0	66.0	27.806	2986.283	0.065	0.93%	25.77°	6.023	86.7265	0.85 42.810
71.1 - 81.0	76.0	14.597	2986.261	0.064	0.49%	25.00°	2.584	40.8092	0.69 18.318
81.3 - 90.9	86.2	7.505	2985.938	0.065	0.25%	22.41°	0.733	12.3593	0.38 5.205
91.0 - 100.8	95.9	4.161	2985.226	0.056	0.14%	20.32°	0.295	4.9852	0.27 2.061
101.1 - 110.9	106.2	2.365	2984.823	0.052	0.08%	18.39°	0.120	2.0358	0.19 0.830
111.0 - 120.5	115.8	1.456	2984.889	0.047	0.05%	17.10°	0.049	0.8372	0.13 0.337
121.0 - 130.5	125.7	0.940	2984.668	0.042	0.03%	15.64°	0.020	0.3447	0.08 0.139
131.0 - 140.9	136.5	0.602	2983.837	0.041	0.02%	14.70°	0.010	0.1747	0.06 0.070
141.0 - 148.6	144.6	0.433	2983.970	0.039	0.01%	14.33°	0.008	0.1297	0.07 0.052
151.6 - 151.6	151.6	0.328	2984.972	0.037	0.01%	14.04°	0.007	0.2452	0.08 0.048

File name: P032389A.BND; size: 27987bytes; written: 3-23-1989 1473 scans

Profile ended: 03-23-1989 08:15:40

Units are meters, PAR: $\mu\text{E}/\text{m}^2$, kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in $\text{nE}/\text{m}^2/\text{s}/\text{str}$ from chlorophyll, Producted production in nM carbon/ m^3/sec .

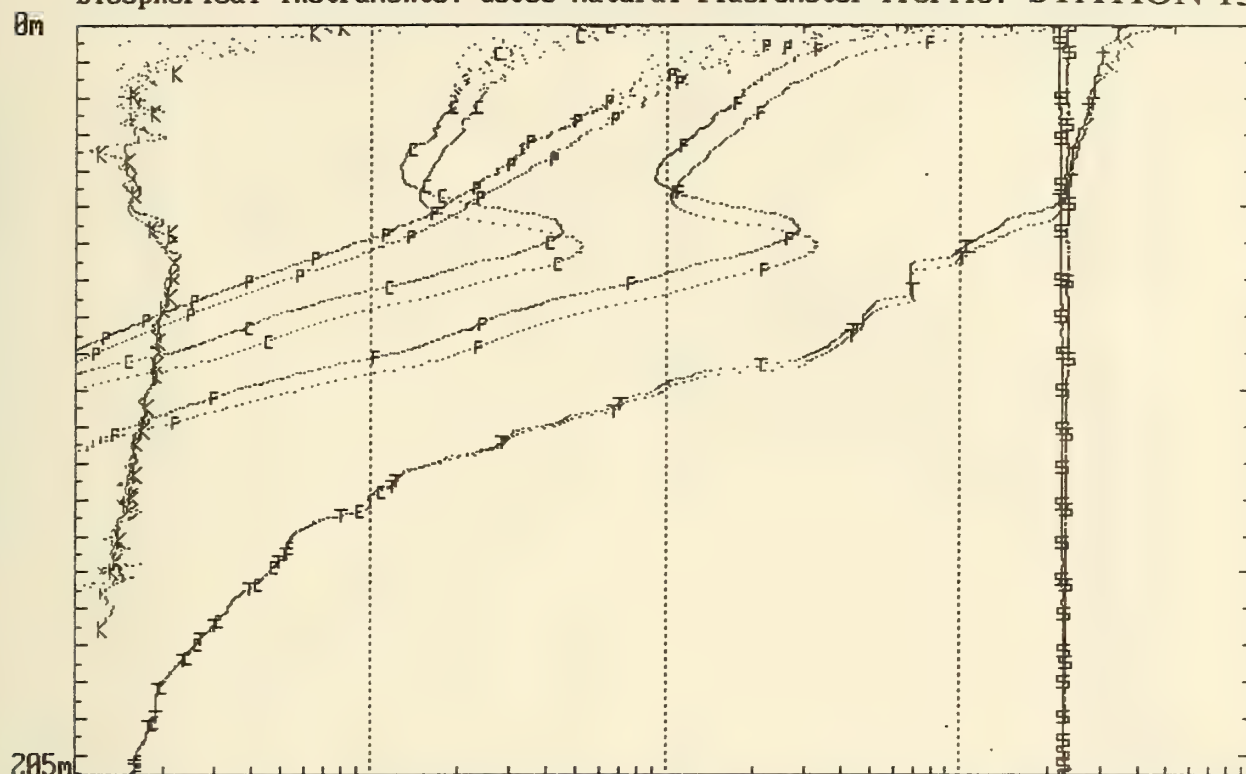
Chlorophyll (Chla) is in mg/m^3 assuming $a_c(\text{PAR}) = .04$ and $Q_E(F) = .045$

Production assumes: $a(683) = .5$, $Q_E(C/F) = 2.4$; $kcf = 133$ 12.63789 to 12.79088

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 13



<.01
 <1 S:Surf PAR
 <.1
 <12°

.1 F:Natural Fluor
 10 P: UW PAR
 1 C:Production
 T:Temperature

1
 100 k:kpar(0-1)
 10
 22°

10 nE/m²/str/s
 1k μE/m²/sec
 100 nMaC/m³/s
 Celsius

100>
 10k>
 1k>
 32°>

Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.3	645.803	2218.847	n.a.	n.a.	30.19°	18.593	0.2	
1.1 - 11.0	5.8	241.266	2230.387	0.132	10.82%	29.63°	6.029	40.9958	0.11 49.690
11.2 - 21.0	16.2	96.307	2229.438	0.054	4.32%	29.29°	2.372	23.7094	0.10 16.543
21.1 - 30.8	25.8	57.882	2225.572	0.053	2.60%	29.13°	1.646	19.4360	0.11 11.428
31.0 - 40.8	35.9	35.506	2230.318	0.041	1.59%	28.92°	1.176	15.4565	0.13 7.999
41.1 - 50.8	46.0	23.022	2207.370	0.047	1.04%	28.75°	1.157	16.6546	0.20 7.956
51.2 - 60.7	55.8	13.567	2238.728	0.068	0.61%	27.80°	2.469	38.9109	0.78 17.652
61.1 - 71.0	66.1	6.198	2243.180	0.082	0.28%	26.53°	1.708	29.2294	1.08 12.483
71.1 - 81.0	76.1	2.746	2240.688	0.076	0.12%	25.80°	0.546	9.7954	0.76 3.956
81.3 - 90.9	86.2	1.316	2243.617	0.069	0.06%	24.97°	0.206	3.6611	0.61 1.474
91.2 - 100.9	96.1	0.674	2247.601	0.066	0.03%	22.81°	0.073	1.2993	0.40 0.517
101.3 - 110.9	106.2	0.360	2248.194	0.058	0.02%	20.74°	0.024	0.4312	0.26 0.171
111.0 - 120.8	116.0	0.211	2249.623	0.050	0.01%	18.92°	0.011	0.1859	0.20 0.074
121.0 - 125.5	122.7	0.140	2227.976	0.046	0.01%	17.61°	0.008	0.1391	0.20 0.052

File name: P032389B.BND; size: 24491bytes; written: 3-23-1989 1289 scans

Profile ended: 03-23-1989 15:13:21

Units are meters, PAR: μE/m², kPAR:1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in nE/m²/s/str from chlorophyll, Produced production in nM carbon/m³/sec.

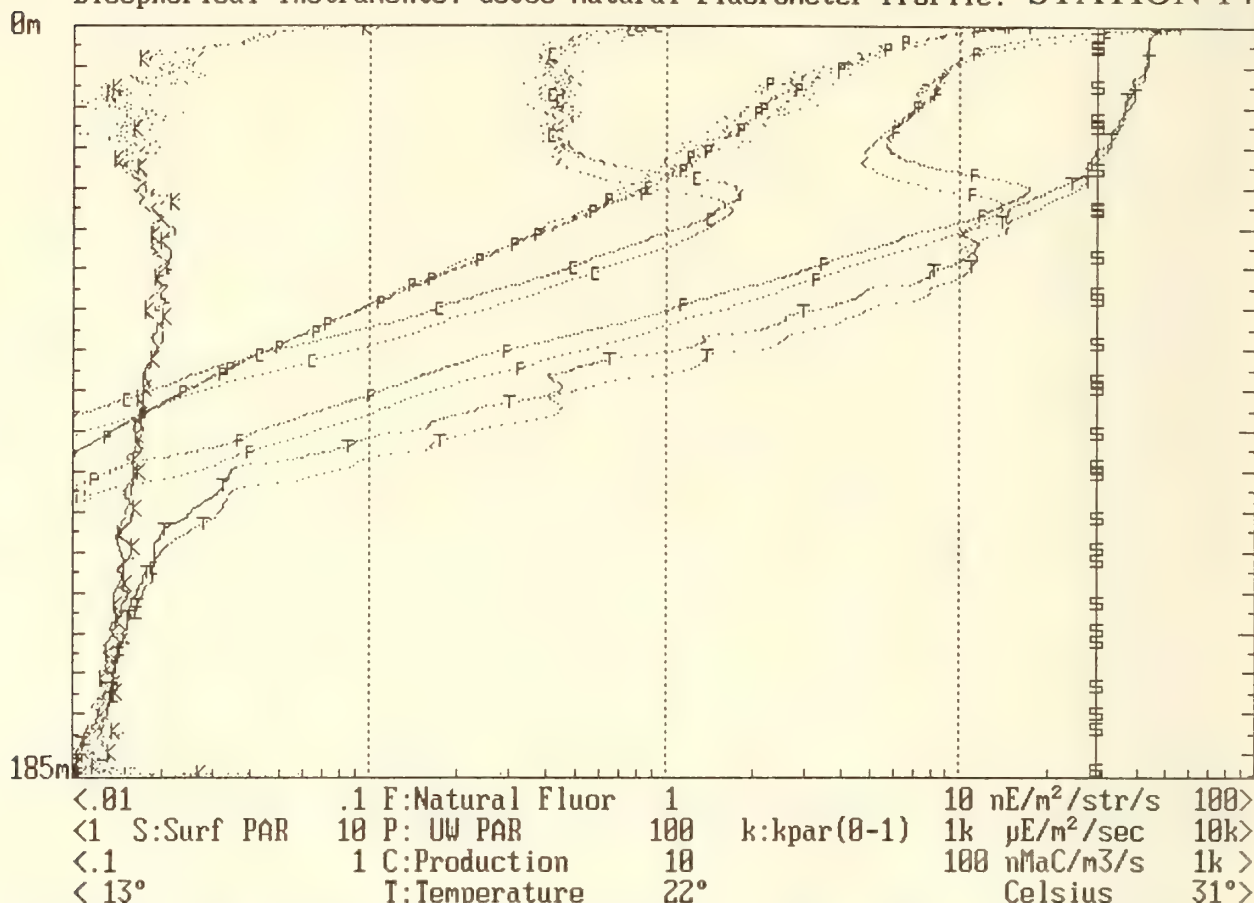
Chlorophyll (Chla) is in mg/m cubed assuming ac(PAR) = .04 and QE(F) = .045

Production assumes: a(683)= .5, QE(C/F)= 2.4; kcf= 133 12.63789 to 12.70892

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 14



Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.3	1377.760	2936.687	n.a.	n.a.	29.52°	49.858	0.2	
1.1 - 10.7	5.7	650.777	2929.908	0.120	22.21%	29.37°	16.100	51.0985	0.10 128.986
11.1 - 21.0	15.9	271.924	2928.913	0.050	9.28%	29.14°	7.966	44.5358	0.12 55.127
21.1 - 30.8	25.9	172.383	2930.736	0.051	5.88%	28.86°	6.033	44.6618	0.14 41.816
31.2 - 40.9	36.0	103.461	2930.549	0.052	3.53%	28.39°	8.946	86.4995	0.36 62.258
41.1 - 50.8	45.8	57.412	2931.687	0.071	1.96%	27.38°	12.624	152.3169	0.89 90.548
51.2 - 60.8	56.0	26.837	2929.372	0.076	0.92%	26.61°	5.329	79.0970	0.79 38.507
61.1 - 70.8	65.8	12.889	2930.208	0.072	0.44%	25.43°	1.965	32.1257	0.60 14.134
71.1 - 80.8	75.9	6.213	2928.934	0.071	0.21%	23.39°	0.649	11.2588	0.41 4.660
81.1 - 90.9	85.9	3.162	2929.286	0.062	0.11%	21.02°	0.205	3.5940	0.25 1.447
91.2 - 100.9	96.0	1.729	2928.108	0.057	0.06%	19.28°	0.076	1.3302	0.17 0.535
101.3 - 110.9	106.1	0.994	2928.529	0.052	0.03%	16.96°	0.029	0.4956	0.11 0.198
111.0 - 120.8	115.9	0.607	2926.115	0.048	0.02%	15.27°	0.011	0.1932	0.07 0.077
121.3 - 128.4	123.9	0.413	2926.140	0.044	0.01%	14.60°	0.008	0.1297	0.07 0.052

File name: P032489A.BND; size: 23256bytes; written: 3-24-1989 1224 scans

Profile ended: 03-24-1989 07:14:33

Units are meters, PAR: μ E/m², kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in nE/m²/s/str from chlorophyll, Producted production in nM carbon/m³/sec.

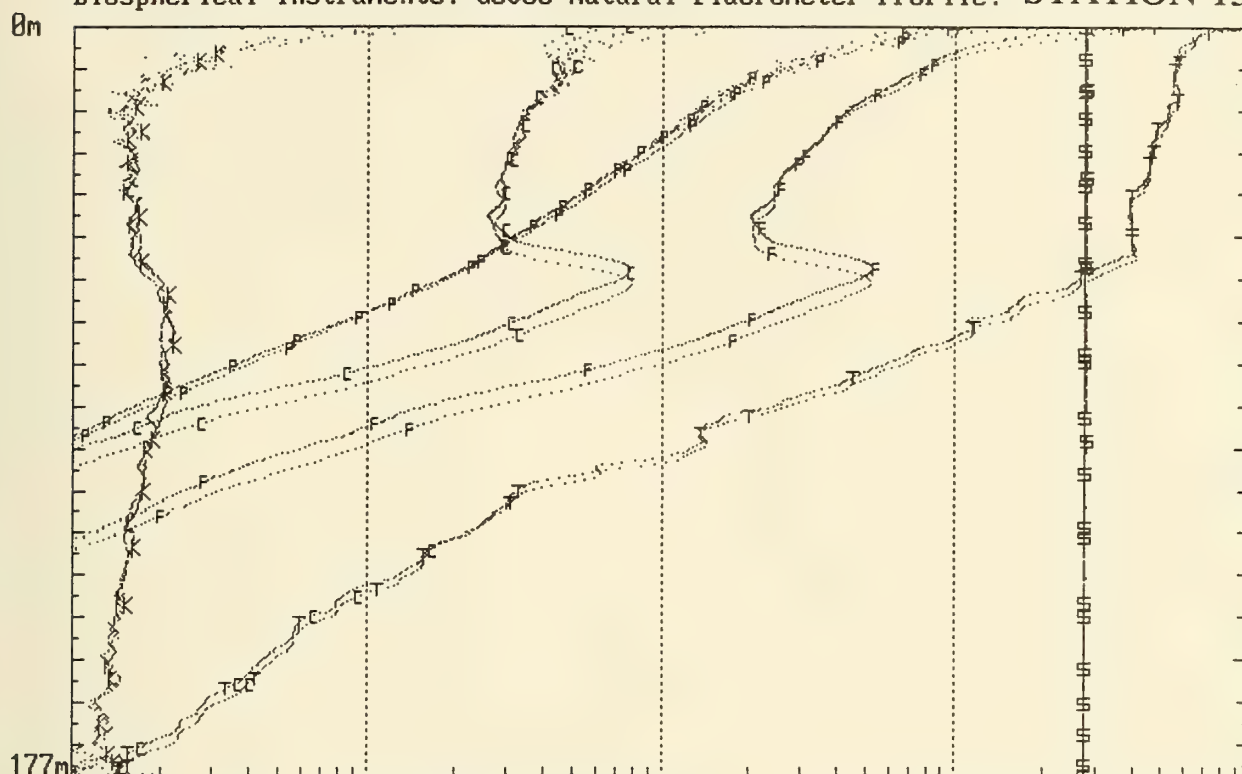
Chlorophyll (Chla) is in mg/m cubed assuming ac(PAR) = .04 and QE(F) = .045

Production assumes: a(683) = .5, QE(C/F) = 2.4; kcf = 133 12.6215 to 12.64336

Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

Biospherical Instruments: Go300 Natural Fluorometer Profile: STATION 15



<.01
 <1 S:Surf PAR 10 P: UW PAR 100 k:kpar(0-1) 1k $\mu\text{E}/\text{m}^2/\text{sec}$ 10k>
 <.1 C:Production 10 100 nMaC/m3/s 1k >
 < 14° T:Temperature 22° Celsius 30°>

Depth range	Mean	PAR	RefPAR	kPAR	% PAR	Temp	LuChl	Prod	Chla
Surface mean:	0.3	1142.073	2755.053	n.a.	n.a.	29.72°	37.118	0.2	
1.2 - 11.0	6.4	428.283	2758.507	0.136	15.53%	29.08°	12.112	56.5281	0.13 99.779
11.2 - 21.0	16.4	170.280	2757.667	0.056	6.17%	28.96°	5.504	41.0312	0.13 38.614
21.1 - 30.8	26.0	107.251	2759.122	0.047	3.89%	28.74°	3.604	33.4948	0.13 24.784
31.0 - 40.9	36.0	65.785	2758.799	0.049	2.38%	28.56°	2.640	29.7162	0.16 18.217
41.1 - 50.8	46.0	39.954	2762.432	0.053	1.45%	28.38°	2.187	28.5178	0.22 15.189
51.0 - 60.8	55.9	23.504	2763.394	0.059	0.85%	28.13°	3.968	57.8882	0.70 27.965
61.1 - 71.0	66.1	11.613	2765.763	0.078	0.42%	26.92°	3.133	51.0778	1.08 22.747
71.1 - 80.8	75.9	5.270	2763.822	0.080	0.19%	25.70°	1.270	22.3037	0.96 9.260
81.1 - 90.7	85.8	2.427	2766.464	0.078	0.09%	24.31°	0.395	7.2096	0.63 2.871
91.0 - 100.9	95.8	1.155	2764.804	0.068	0.04%	22.71°	0.113	2.0593	0.38 0.807
101.1 - 110.9	106.1	0.598	2763.814	0.060	0.02%	21.05°	0.041	0.7306	0.26 0.288
111.2 - 120.7	116.0	0.340	2764.081	0.050	0.01%	19.70°	0.018	0.3122	0.20 0.124
121.0 - 127.9	123.7	0.239	2764.209	0.049	0.01%	18.96°	0.009	0.1693	0.15 0.065

File name: P032489B.BND; size: 20292bytes; written: 3-24-1989 1068 scans

Profile ended: 03-24-1989 14:04:45

Units are meters, PAR: $\mu\text{E}/\text{m}^2$, kPAR: 1/meters, Temp Degrees C.

Diffuse attenuation coefficient for PAR (Kpar) in 1/meters, 15 point smooth.

Natural Fluorescence in $\text{nE}/\text{m}^2/\text{s}/\text{str}$ from chlorophyll, Produced production in nM carbon/ m^3/sec .

Chlorophyll (Chla) is in mg/m^3 cubed assuming $\text{ac}(\text{PAR}) = .04$ and $\text{QE}(\text{F}) = .045$

Production assumes: $\text{a}(683) = .5$, $\text{QE}(\text{C/F}) = 2.4$; $\text{kcf} = 133$ 12.6215 to 12.68707

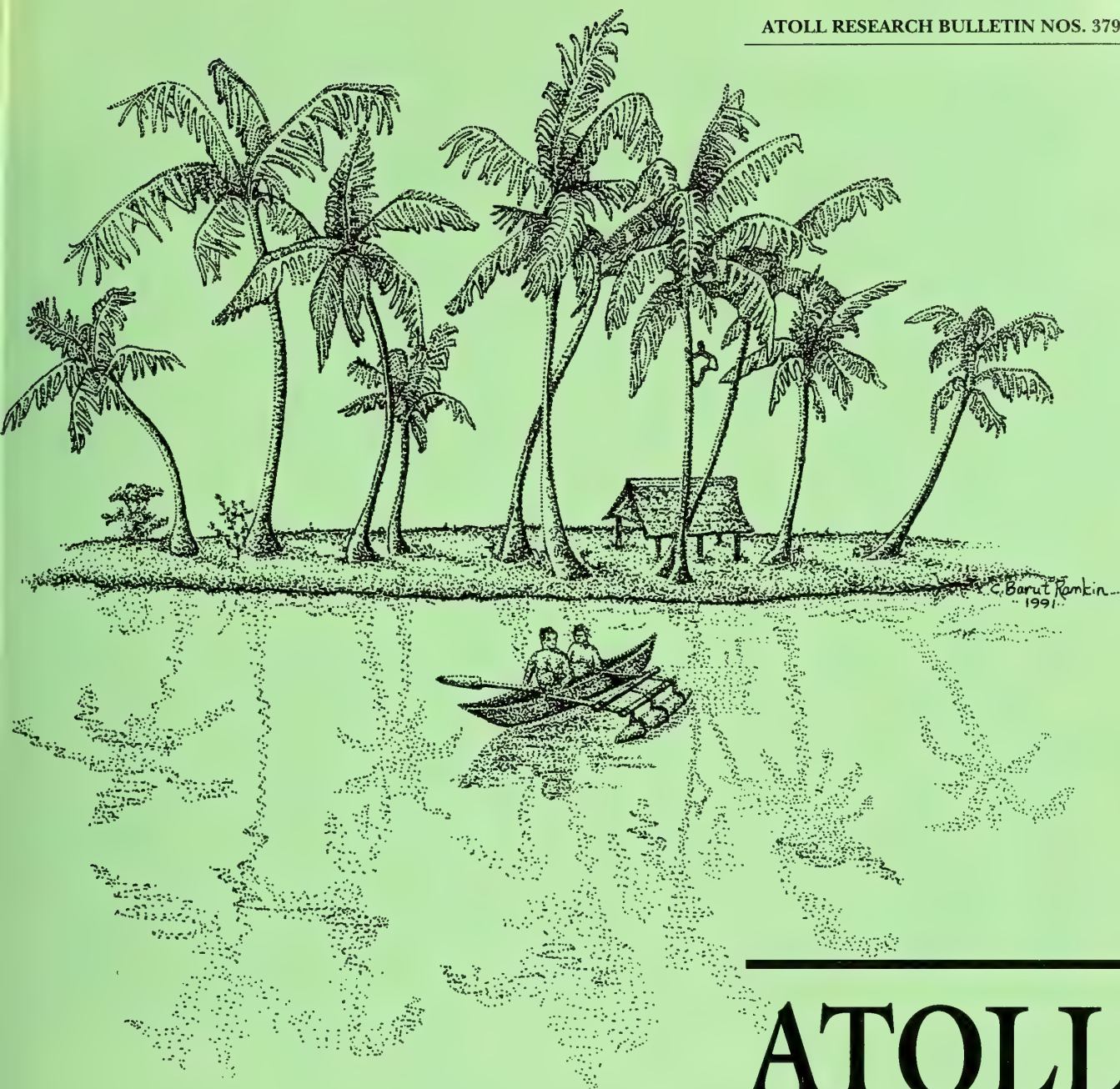
Battery voltage range during profile

Prototype #1:1032 (Delrin) Calibration of 4/13/89

ATOLL RESEARCH BULLETIN

NOS. 365-378

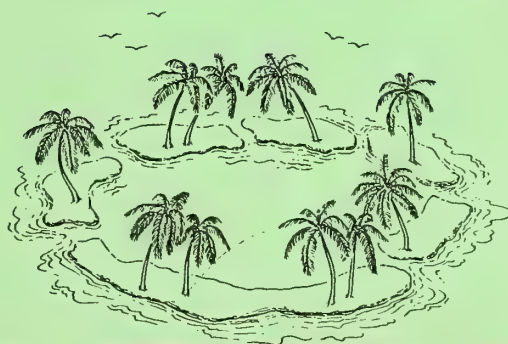
- NO. 365. INTRODUCTION TO THE SOVIET-AMERICAN EXPEDITION TO THE SEYCHELLES ISLANDS
BY E.A. TITLYANOV, M.M. LITTLER AND D.S. LITTLER
- NO. 366. CHARACTERISTICS OF OCEANOGRAPHIC PROCESSES ON REEFS OF THE SEYCHELLES ISLANDS
BY A.V. NOVOZHILOV, Y.N. CHERNOVA, I.A. TSUKUROV, V.A. DENISOV AND L.N. PROPP
- NO. 367. OCTOCORALLIA FROM THE SEYCHELLES ISLANDS WITH SOME ECOLOGICAL OBSERVATIONS
BY A.N. MALYUTIN
- NO. 368. SPECIES COMPOSITION AND ABUNDANCE OF CORALS AND OTHER INVERTEBRATES ON THE REEFS OF THE SEYCHELLES ISLANDS
BY N.I. SELIN, Y.Y. LATYPOV, A.N. MALYUTIN AND L.N. BOLSHAKOVA
- NO. 369. SPECIES COMPOSITION, DISTRIBUTION AND ABUNDANCE OF ALGAE AND SEAGRASSES OF THE SEYCHELLES ISLANDS
BY A.A. KALUGINA-GUTNIK, L.P. PERESTENKO AND T.V. TITLYANOVA
- NO. 370. FOULING COMMUNITIES OF THE SEYCHELLES ISLANDS
BY A.Y. ZVYAGINTSEV AND V.V. IVIN
- NO. 371. NITRIFICATION, DENITRIFICATION AND NITROGEN FIXATION IN BOTTOM SEDIMENTS OF LAGOONS OF THE SEYCHELLES ISLANDS
BY M.V. PROPP, V.S. ODINTSOV AND L.N. PROPP
- NO. 372. NITROGEN FIXING ACTIVITY ASSOCIATED WITH SUBTIDAL MACROPHYTES OF THE SEYCHELLES ISLANDS
BY V.S. ODINTSOV
- NO. 373. PHOTOSYNTHESIS IN COMMON MACROPHYTE SPECIES IN THE INTERTIDAL AND UPPER SUBTIDAL ZONES OF THE SEYCHELLES ISLANDS
BY E.A. TITLYANOV, K.Y. BIL', P.V. KOLMAKOV, A.A. LAPSHINA AND T.R. PÄRNIK
- NO. 374. PHOTOSYNTHESIS VS. IRRADIANCE CURVES FOR SIX SPECIES OF MACROALGAE FROM THE SEYCHELLES ISLANDS UNDER FOUR LEVELS OF NUTRIENT ENRICHMENT
BY M.M. LITTLER AND D.S. LITTLER
- NO. 375. LIGHT AND TEMPERATURE DEPENDENCE OF OXYGEN EXCHANGE, CARBON ASSIMILATION AND PRIMARY PRODUCTION IN *THALASSODENDRON CILIATUM* BLADES
BY E.A. TITLYANOV, V.A. LELETKIN, K.Y. BIL', P.V. KOLMAKOV AND E.G. NECHAI
- NO. 376. PHOTOSYNTHESIS OF THE SEAGRASS *THALASSODENDRON CILIATUM*; LEAF MORPHOLOGY AND CARBON METABOLISM
BY T.R. PÄRNIK, K.Y. BIL', P.V. KOLMAKOV AND E.A. TITLYANOV
- NO. 377. PHOTOSYNTHETIC PRODUCTS OF ZOOXANTHELLAE OF THE REEF-BUILDING CORALS *STYLOPHORA PISTILLATA* AND *SERIATOPORA COLIENDRUM*
BY K.Y. BIL', P.V. KOLMAKOV AND L. MUSCATINE
- NO. 378. ESTIMATES OF INDIAN OCEAN PRODUCTIVITY USING NATURAL FLUORESCENCE
BY P. DUSTAN



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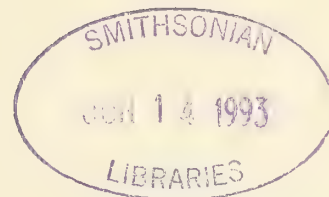
ATOLL RESEARCH BULLETIN

NOS. 379-389

- NO. 379. MONSOONAL UPWELLING AND EPISODIC *ACANTHASTER* PREDATION AS PROBABLE CONTROLS OF CORAL REEF DISTRIBUTION AND COMMUNITY STRUCTURE IN OMAN, INDIAN OCEAN
BY PETER W. GLYNN**
- NO. 380. CORAL REEFS OF THE SULTANATE OF OMAN
BY RODNEY V. SALM**
- NO. 381. THE HETEROPTERA OF ALDABRA ATOLL AND NEARBY ISLANDS, WESTERN INDIAN OCEAN, PART 2. FRESHWATER HETEROPTERA (INSECTA): CORIXIDAE, NOTONECTIDAE, VELIIDAE, GERRIDAE, AND MESOVELIIDAE
BY DAN A. POLHEMUS**
- NO. 382. STUDIES ON LITTORAL AND SUBLITTORAL MACROPHYTES AROUND THE MAURITIUS COAST
BY T. G. JAGTAP**
- NO. 383. STUDIES ON THE BIOLOGY AND ECOLOGY OF THE INTERTIDAL ANIMALS OF CHICHIJIMA ISLAND IN THE OGASAWARA (BONIN) ISLANDS
BY AKIRA ASAKURA, SHIROU NISHIHAMA, AND YASUO KONDO**
- NO. 384. PLANT COLONIZATION OF A RUBBLE BANK ON HERON ISLAND, GREAT BARRIER REEF, AUSTRALIA
BY R. W. ROGERS**
- NO. 385. IMPACT OF TOURISM-RELATED FISHING ON *TRIDACNA MAXIMA* (MOLLUSCA, BIVALVIA) STOCKS IN BORA-BORA LAGOON (FRENCH POLYNESIA)
BY S. PLANES, C. CHAUVET, J. BALDWIN, J. BONVALLOT, Y. FONTAINE-VERNAUDON, C. GABRIE, P. HOLTHUS, C. PAYRI, AND R. GALZIN**
- NO. 386. MANGROVE SWAMPS IN BERMUDA
BY MARTIN L. H. THOMAS**
- NO. 387. DISTRIBUTIONAL CONTROL OF SEAGRASSES BY LIGHT AVAILABILITY, TWIN CAYS, BELIZE, CENTRAL AMERICA
BY J. A. CALEM AND J. W. PIERCE**
- NO. 388. SOME REEFS AND CORALS OF ROATAN (HONDURAS), CAYMAN BRAC, AND LITTLE CAYMAN
BY DOUGLAS P. FENNER**
- NO. 389. CLASSIFICATION OF NON-MARINE ECOSYSTEMS
BY F. RAYMOND FOSBERG AND SAM H. PEARSALL III**

NEWS AND COMMENTS

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ATOLL RESEARCH BULLETIN

NO. 379

**MONSOONAL UPWELLING AND EPISODIC *ACANTHASTER*
PREDATION AS PROBABLE CONTROLS OF CORAL REEF
DISTRIBUTION AND COMMUNITY STRUCTURE
IN OMAN, INDIAN OCEAN**

BY

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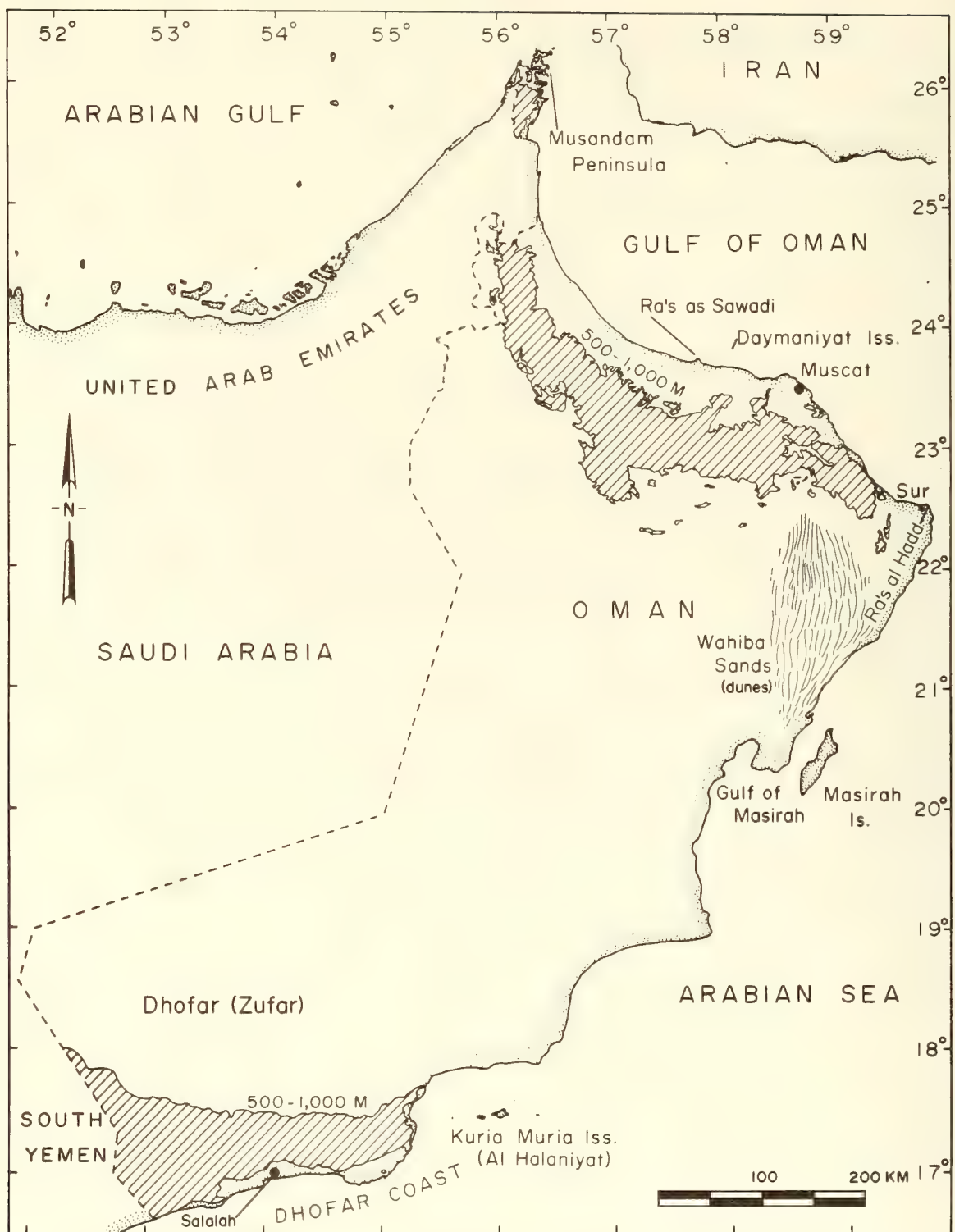


Figure 1. Sultanate of Oman and surrounding waters. After the topographic map of Shell Markets (Middle East) Ltd., 1977, scale 1:1,000,000. Mountains (hatched areas) only shown for Oman.

MONSOONAL UPWELLING AND EPISODIC *ACANTHASTER*

PREDATION AS PROBABLE CONTROLS OF CORAL REEF

DISTRIBUTION AND COMMUNITY STRUCTURE

IN OMAN, INDIAN OCEAN

BY

PETER W. GLYNN

ABSTRACT

Fringing and patch coral reefs are present on the Arabian (Persian) Gulf shores of northern Oman (Musandam) and in the Gulf of Oman, notably off the Daymaniyat Islands and in the Capital (Muscat) area. Coral reefs are generally absent from the Arabian Sea coast of southern Oman, most likely a result of monsoon-induced upwelling. However, fringing reefs are present on the northwest (leeward) side of Masirah Island and on the mainland opposite, both areas that are partly sheltered from open coast upwelling. *Acanthaster planci* was observed in the coral rich Gulf of Oman only, where it caused widespread and selective coral mortality during a population outbreak. Starting in 1978-79, with diminishing effects to 1982, coral reefs with high acroporid coral cover experienced high mortalities with virtually all *Acropora* spp. eliminated on many reefs. Reefs with high pocilloporid coral cover largely escaped predation, probably because *Acanthaster* encountered difficulties in traversing continuous stands of this coral: the coral's nematocysts and the presence of symbiotic crustacean guards deter the starfish. Thus, where environmental conditions are suitable for reef development, sporadic, high level *Acanthaster* predation can modify coral community structure through the differential survival of coral prey and hence lead to the development of *Acanthaster* resistant reef types.

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INTRODUCTION

This paper grew out of surveys conducted in the Sultanate of Oman to assess damage to coral reefs caused by the starfish corallivore *Acanthaster planci* (Linnaeus). The Ministry of Agriculture and Fisheries (MAF) received reports during 1978-1980 indicating that population outbreaks of *A. planci* were causing high mortalities among reef corals in the Daymaniyat Islands and along the coast near Muscat (Gulf of Oman), also known as the Capital area (Figure 1). Since so little was known of the extent of coral community development and the distribution of *A. planci* in Oman at that time, the MAF decided to extend the survey to four other areas in Oman, including (1) the Musandam Peninsula at the southern end of the Arabian (Persian) Gulf, (2) Ra's al Hadd (east of Sur), which borders the Gulf of Oman and Arabian Sea, (3) Masirah Island, and (4) the coastal area of Dhofar (Zufar), the latter two areas in the Arabian Sea.

When the present field studies were conducted in 1982 the only information available on Omani corals was that in Rosen (1971) and Cornelius et al. (1973), both of whom reported on corals in the Musandam Peninsula region. Fifteen reef-coral genera were listed by Rosen (1971), and Cornelius et al. (1973) claimed that 'true reefs', i.e. structures with significant framework development, were absent from this region. Stoddart's (1971a) synoptic map of the distribution of coral reefs in the Indian Ocean shows coral reefs present only in the Capital area and along the Arabian Sea coast of Oman.

Several important studies on the corals and coral reefs of Oman have appeared since the early 1980s. In the UNEP/IUCN (1988) handbook of Coral Reefs of the World (vol. 2), 11 studies were listed that dealt with reef corals from the coastal areas of Oman. These papers were published mainly as technical reports between 1983-1986. The studies of Green and Keech (1986), Glynn (1987), Sheppard (1988), and Sheppard and Salm (1988), generally more accessible than the technical reports, provide information on the general biology, systematics and ecology of Omani corals and coral reefs. More recently, Sheppard et al. (1992) present a general account of coral reef ecology in the Arabian region, and the following article by Salm (1993) in this issue offers new information on various disturbances to coral reefs and the extent of reef development along the Arabian Sea coast of Oman.

Coral communities and coral reefs in the Gulf of Oman and Arabian Sea experience upwelling. Strong upwelling impacts corals and restricts reef development. For example, coral reef development is limited or absent in upwelling areas in the eastern Pacific (Dana, 1975; Glynn and Wellington,

1983), Marquesas Islands (Ladd, 1971; Sournia, 1976), and off equatorial west Africa (Laborel, 1974) and the Venezuelan coast (Antonius, 1980). When sea water temperatures fall below about 18°C for an extended period (2-4 weeks or longer) corals suffer partial or total tissue death (Glynn and Stewart, 1973; Birkeland, 1977; Glynn and D'Croz, 1990) and can be competitively displaced by macroalgae, which usually show accelerated growth as a result of increased nutrients. The elevated nutrient concentrations in upwelled waters around coral reefs (Sournia, 1976), as well as in waters bathing many high latitude reefs (Johannes et al., 1983; Hatcher, 1985, 1991; Coles, 1988), favor the growth of phytoplankton and macroalgae. Although the monsoonal upwelling system of the Arabian Sea coast of Oman has been well known in general terms (Currie et al., 1973; Bruce, 1974), only during the past decade have studies revealed detailed patterns of coastal upwelling (Elliott and Savidge, 1990; Savidge et al., 1990; Brock and McClain, 1992; Brock et al., 1992). This study contrasts thermal environments in the Gulf of Oman and Arabian Sea, derived from long-term ship measurements and recent remote sensing observations, to reveal the influence of upwelling on the spatial distribution of Omani coral reefs.

Several recent studies have demonstrated a strong effect of *Acanthaster* predation on Indo-Pacific coral communities, especially at high corallivore population densities (Potts, 1982; Moran, 1986; Glynn, 1990a). The effects of *Acanthaster* on corals in Oman were unknown before the 1980s. I observed relatively large numbers of *Acanthaster* in the Gulf of Oman in 1982, evidently the remnants of a population outbreak that occurred there between 1978-80. From observations of extensive, recently killed corals and the feeding activities of *Acanthaster*, this predator can exercise a strong influence on coral survivorship in some areas of Oman. Further, prey selectivity data revealed that *Acanthaster* also can have a significant effect in altering the species composition of coral communities (Glynn, 1987). In this paper, I will evaluate the relative importance of upwelling and predation respectively in regulating coral community structure and in controlling the distribution of coral reefs under upwelling and non-upwelling conditions.

METHODS

The coastal surveys in Oman, from the Musandam Peninsula in the north to the Dhofar Province in the south (Figure 1), were conducted from 20 September to 25 October, 1982. Coral habitats were located with the help of personnel from the MAF, by local fishermen and sports divers, from

hydrographic charts, by surveying shorelines from elevated sites (hill tops and towers), and by aerial reconnaissance. Work underwater was carried out by surface diving and scuba during daylight hours from small boats that could be maneuvered near shore. The nature and extent of coral cover, and the physical dimensions of coral framework construction were determined at each station. Only crude estimates of reef framework thickness were obtained. On small, thin reefs the thickness of coral buildups was estimated visually and by modest surface excavation. On larger reefs, the depth range of vertical buildups was estimated from the depth differences of the reef crest or reef flat and the reef base, measured with a standard, calibrated depth gauge. Bottom areas were measured with a chain marked at 1 m intervals. Field sketches of some reefs were made, which emphasized coral zonation and vertical relief. Reef dimensions also were estimated from near-vertical aerial photographs taken at 600 m elevation. The sizes of reef features in the aerial photographs were determined from ground-truth measurements and with reference to distance scales on hydrographic charts.

Wainwright's (1965) distinction between coral communities and structural coral reefs was followed in this study. That is, coral formations were recognized as true reefs when it could be determined that corals, calcareous algae and other associated organisms were actively contributing to the accumulation of interlocking framework structures. These structures form significant topographic features, which result from the skeletal accumulation of modern calcifying organisms (Stoddart, 1969). No Pleistocene reef structures were found in this study. The recognition of coral reefs by Sheppard and Salm (1988) was more restrictive than the above, requiring the presence of a "...characteristic reef topography of a horizontal reef flat at low tide and a reef slope.". I prefer Wainwright's (1965) definition because several relatively large coral buildups observed in this study (4-6 m thick, 1-2 ha) lacked obvious reef flats, but otherwise would qualify as true structural reef formations.

Coral species composition and percent live cover were determined from 10 m-long chain transects and from 0.25 m² point quadrat counts. Chain transects (with 1.4 cm links) were positioned along isobath contours in all coral zones (Porter, 1972a). Chain transect sampling intervals of 5, 10 and 15 m were used depending on reef widths. Also, 6 to 7 transects (with 710 sampling points each) were sampled on each reef. Additional sampling on reefs was performed with quadrats, each with 16 uniformly spaced sampling points (Glynn, 1987). Usually each reef zone was sampled with 10 haphazardly located quadrats. Species diversity, employing the Shannon-Wiener index (H' , see Pielou, 1977), was calculated for each zone. Coral species and colony condition (i.e., live, eaten, recently dead, etc.), and the general substrate type (i.e., algae, sponge, soft coral, bryozoans, sand, rock, etc.) were recorded. Voucher specimens of questionable or unknown

species were collected for later identification (see Table 1). John W. Wells identified all specimens except *Acropora* spp. and this collection was donated to the U.S. National Museum, Smithsonian Institution, Washington, D.C. Carden C. Wallace identified *Acropora* species and these were deposited in the collections of the Queensland Museum, North Queensland Branch, Townsville, Australia. A total of 75 sites were surveyed in this study. Their locations, enumerated chronologically, are shown in Figures 2-7. Site 24 (Ra's as Sawadi) was located about 85 km west of Muscat. Surface sea water temperatures were measured with a calibrated mercury thermometer at Arabian Sea sites, and horizontal water visibility and sea state also were noted.

Adult *Acanthaster* were located by swimming over coral substrata and searching under corals and in other cryptic habitats. The search effort was intensified in areas with presumed feeding scars. No other corallivore was found in Oman that produces a feeding scar similar to that of *Acanthaster*. An effort was made to find juvenile *Acanthaster* by searching with scuba in

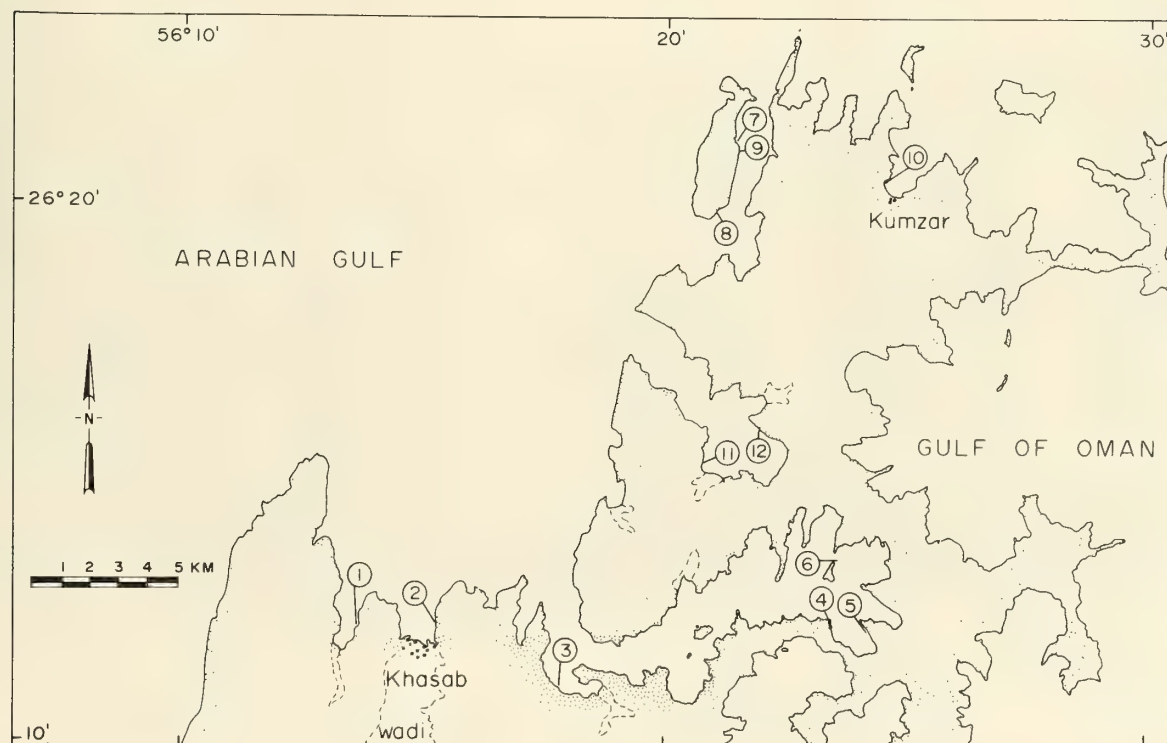


Figure 2. Location of sites surveyed on the Musandam Peninsula, northern Oman. From chart of Oman and United Arab Emirates (Kumzar), scale 1:100,000, series K668, editions 4-GSGS and 2-GSGS. Director of Military Survey, Ministry of Defence, United Kingdom, 1975.

Table 1. Zooxanthellate scleractinians identified from voucher specimens collected at the various localities indicated. M, Musandam; C, Capital area; R, Ra's Abu Da'ud to Ra's al Hadd; MR, Masirah; D, Dhofar.

Family	Species	Locality			
		M	C	R	D
Thamnasteriidae	<i>Psammodora contigua</i> (Esper)	+	+		
Pocilloporidae	<i>Pocillopora damicornis</i> (Linnaeus)	+	+		
	<i>Stylophora erythraea</i> von Marenzeller				+
	<i>Stylophora pistillata</i> (Esper)	+	+		
	<i>Stylophora pistillata</i> (Esper) <i>mordax</i> (palmata) form			+	
	<i>Stylophora subseriata</i> (Ehrenberg)	+			+
Acroporidae	<i>Acropora aspera</i> (Dana)				
	<i>Acropora cytherea</i> (Dana)	+	+		+
	<i>Acropora glauca</i> (Brook)				+
	<i>Acropora cf. glauca</i> (Brook)		+		+
	<i>Acropora haimiei</i> (Milne Edwards & Haime)	+			
	<i>Acropora nasuta</i> (Dana)	+	+		
	<i>Acropora pharaonis</i> (Milne Edwards & Haime)	+	+		
	<i>Acropora cf. selago</i> (Studer)	+			
	<i>Acropora valida</i> (Dana)	+			
	<i>Acropora</i> sp.	+	+		
	<i>Astreopora myriophthalma</i> (Lamarck)		+		
	<i>Montipora cristagalli</i> (Ehrenberg)			+	
	<i>Montipora effusa</i> (Dana)		+		
	<i>Montipora foliosa</i> (Pallas)			+	
	<i>Montipora gracilis</i> Klunzinger	+	+		+
	<i>Montipora laevis</i> Bernard	+		+	
	<i>Montipora scutata</i> Bernard			+	
	<i>Montipora tuberculosa</i> (Lamarck)		+		
	<i>Montipora venosa</i> (Ehrenberg)			+	
	<i>Montipora cf. M. multiformis</i> Bernard			+	+
	<i>Montipora cf. M. solanderi</i> Bernard			+	
Agariciidae	<i>Pavona angularis</i> Klunzinger			+	
	<i>Pavona cactus</i> (Forskaal)	+			
Siderastreidae	<i>Anomastrea irregularis</i> von Marenzeller		+		
	<i>Coscinaraea monile</i> (Forskaal)				+

Table 1 - continued

		M	C	R	MR	D
Siderastreidae	<i>Siderastrea lilacea</i> Klunzinger				+	
Poritidae	<i>Goniopora savignyi</i> Dana	+	+		+	
	<i>Porites cylindrica</i> Dana				+	
	<i>Porites columnaris</i> Klunzinger	+				
	<i>Porites solida</i> (Forskaal)				+	
	<i>Porites cf. P. cocosensis</i> Wells		+		+	
Faviidae	<i>Cyphastrea chalcidicum</i> (Forskaal)		+			
	<i>Cyphastrea microphthalma</i> (Lamarck)	+				
	<i>Cyphastrea serailia</i> (Forskaal)		+		+	+
	<i>Echinopora hirsutissima</i> Milne Edwards & Haime		+			
	<i>Echinopora lamellosa</i> (Esper)	+				
	<i>Favia favius</i> (Forskaal)				+	
	<i>Favia pallida</i> (Dana)					+
	<i>Favites abdita</i> (Ellis & Solander)				+	+
	<i>Favites complanata</i> (Ehrenberg)				+	+
	<i>Favites pentagona</i> (Esper)			+	+	+
	<i>Favites cf. F. spinosa</i> (Klunzinger)	+	+			
	<i>Leptastrea transversa</i> Klunzinger	+	+			
	<i>Platygyra rustica</i> (Dana)	+				
	<i>Platygyra sinensis</i> (Milne Edwards & Haime)	+			+	+
	<i>Plesiastrea versipora</i> (Lamarck)		+			
Oculinidae	<i>Galaxea astreata</i> (Lamarck)		+			
Merulinidae	<i>Hydnophora exesa</i> (Pallas)	+			+	+
	<i>Hydnophora microconos</i> (Lamarck)		+	+		
Mussidae	<i>Acanthastrea echinata</i> (Dana)	+	+		+	
	<i>Symphyllia radians</i> Milne Edwards & Haime	+		+		
Pectiniidae	<i>Echinophyllia aspera</i> Ellis & Solander		+			
	<i>Oxypora lacera</i> (Verrill)	+	+			
Dendrophylliidae	<i>Turbinaria crater</i> (Pallas)		+			+
	<i>Turbinaria peltata</i> (Esper)	+	+			
	<i>Turbinaria cf. T. calicularis</i> Bernard				+	

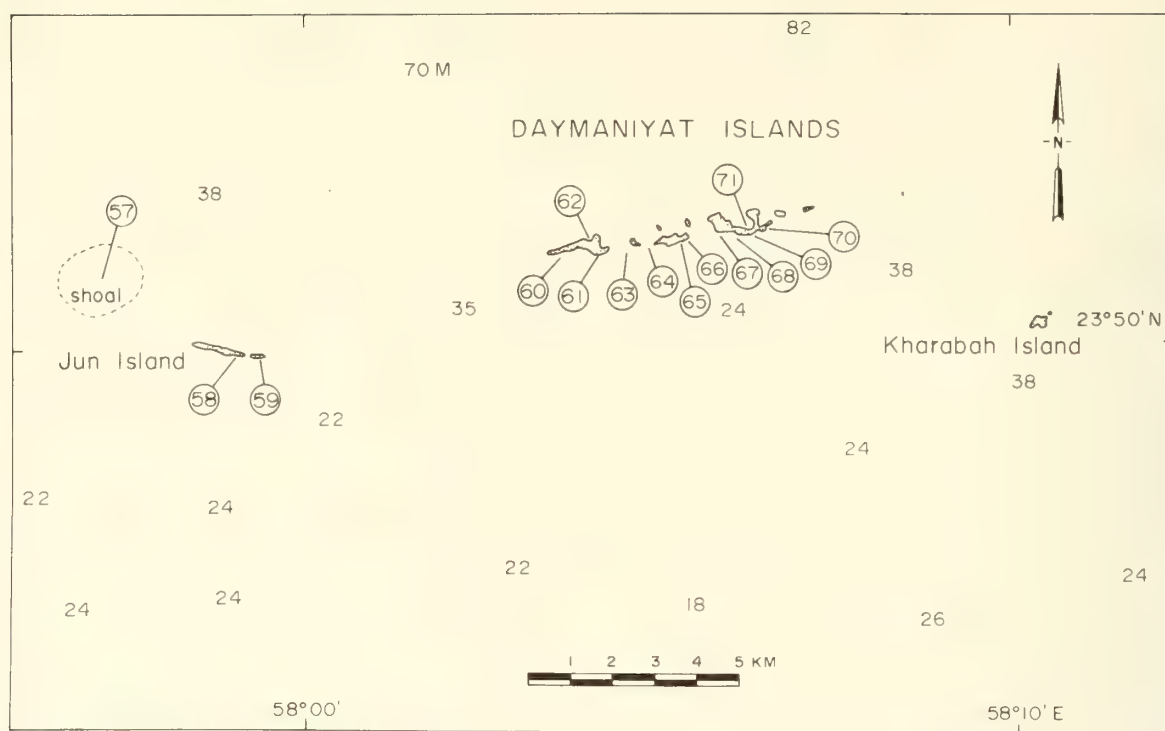


Figure 3. Location of sites surveyed in the Daymaniyat Islands, Gulf of Oman. Map sketched and enlarged from chart published by D Survey, scale 1:100,000, Ministry of Defence, United Kingdom, 1971. Soundings (in m) from marine chart 2851, Masirah to Ruus al Jibal, Admiralty, London, 9 May 1952.

the small cavities of live and dead corals, by searching in coral rubble, and by lifting and examining the undersurfaces of large, live and dead corals. The search effort was recorded in man-hours. Starfish that could be lifted from the substrate were measured in a relaxed state with a cm rule. Both total (arm tip to arm tip) and disc diameters were measured. Coral species prey were noted and 80 point counts of potential prey in the vicinity of feeding *Acanthaster* were recorded as described in Glynn (1987).

Sea surface temperature (SST) data from Nansen casts, spanning the period 1933-1979, were obtained from the National Oceanographic Data Center (NOAA), Washington, D.C. The temperature measurements were generally recorded to the 0.01 place and probably have a minimum precision of $\pm 0.1^{\circ}\text{C}$. Monthly SST plots were constructed by manual contouring.

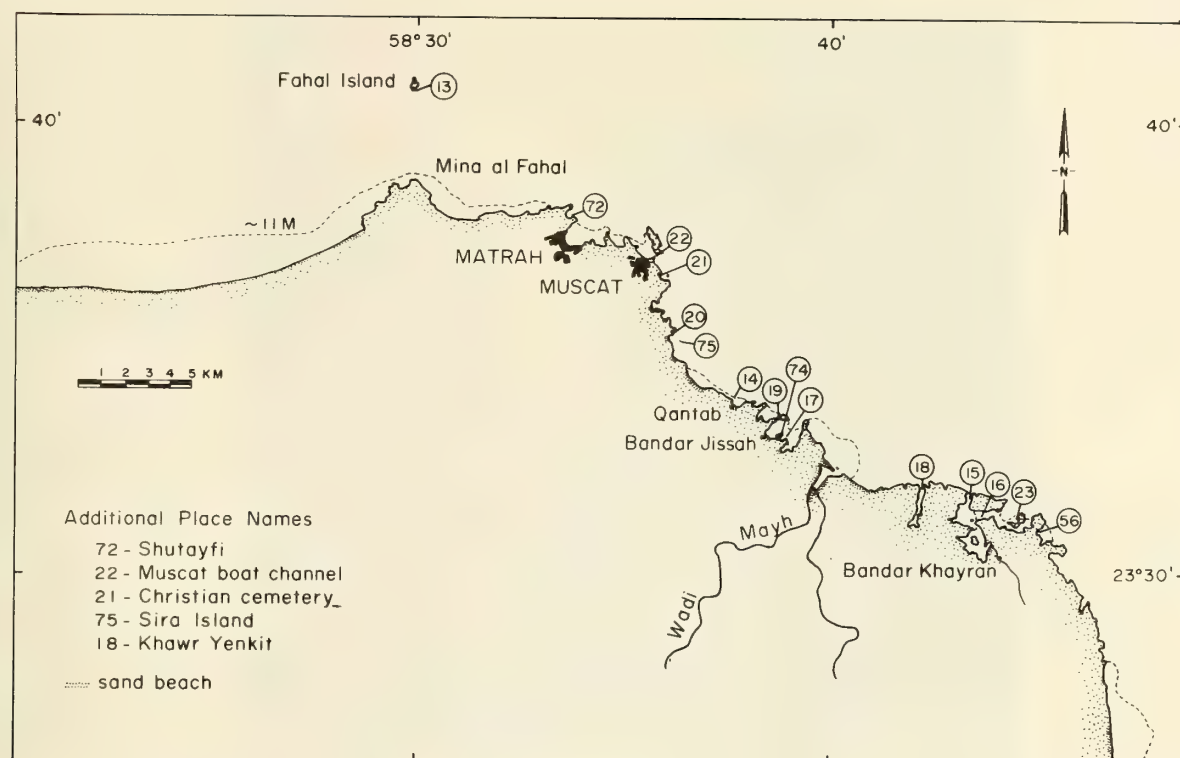


Figure 4. Location of sites surveyed in the Capital (Muscat) area, Gulf of Oman. Dark patches at Matrah and Muscat indicate areas of high population density. After Admiralty Chart 3522, Gulf of Oman, London, 1967.

Satellite infra-red data from 1988 and 1989 were analyzed to reveal near-shore SST patterns and the location of thermal fronts during the summer monsoon season. The time series includes observations from late May to late September, obtained from the Advanced Very High Resolution Radiometer (AVHRR), Local Area Coverage (LAC) data. SST was calculated using a multispectral algorithm described by McClain et al. (1985). These data are archived in the Division of Meteorology and Physical Oceanography, Rosenstiel School of Marine and Atmospheric Science. The NOAA satellite carrying the AVHRR was located in a sun-synchronous polar orbit with ascending passes at approximately 0300 and 1500 (± 50 min.) local sun time. The early morning passes usually provided the clearest images. All SST imagery was mapped to a fixed geographic grid covering the area 55-64°E, 18-26°N with a spatial resolution of approximately 2 km. Detailed analyses were confined to 1° square grids centered over Masirah Island and the Muscat area, and a 6° rectangular grid centered over the Gulf of Oman-Arabian Sea boundary [see Remote sensing data (1988, 1989) below].

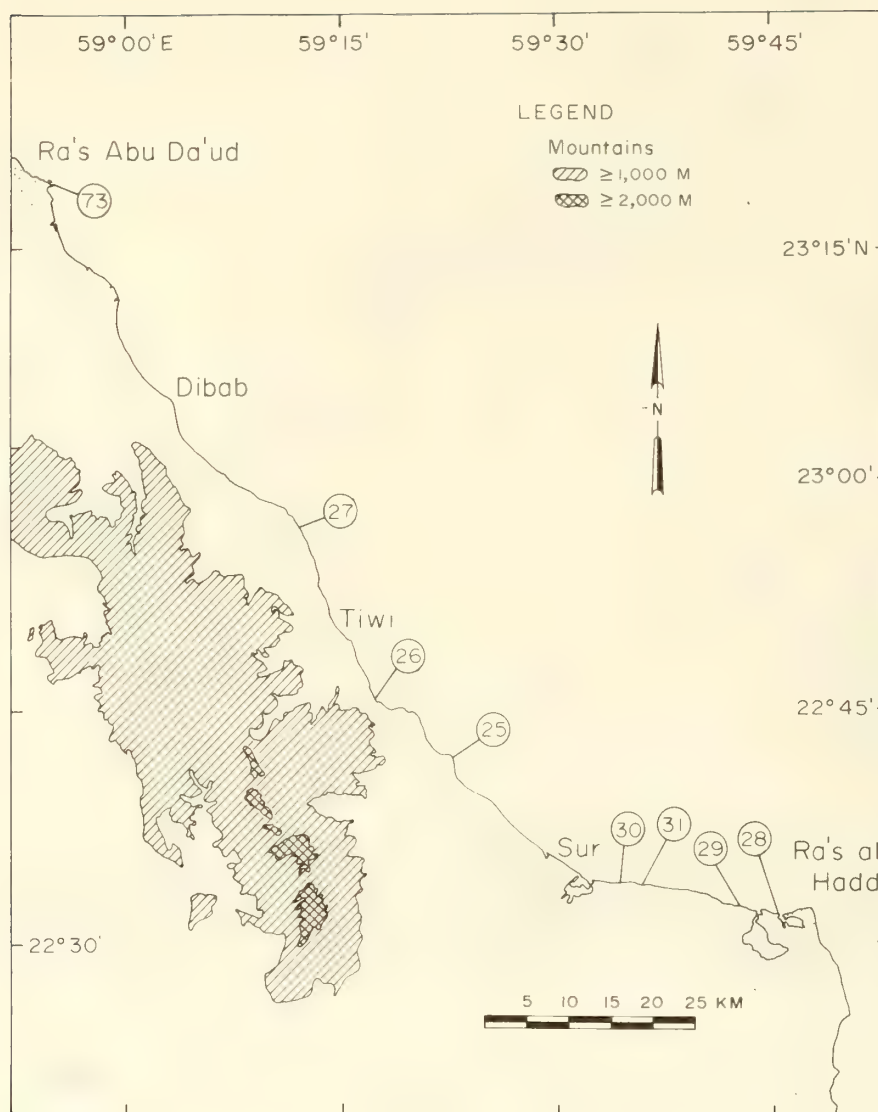
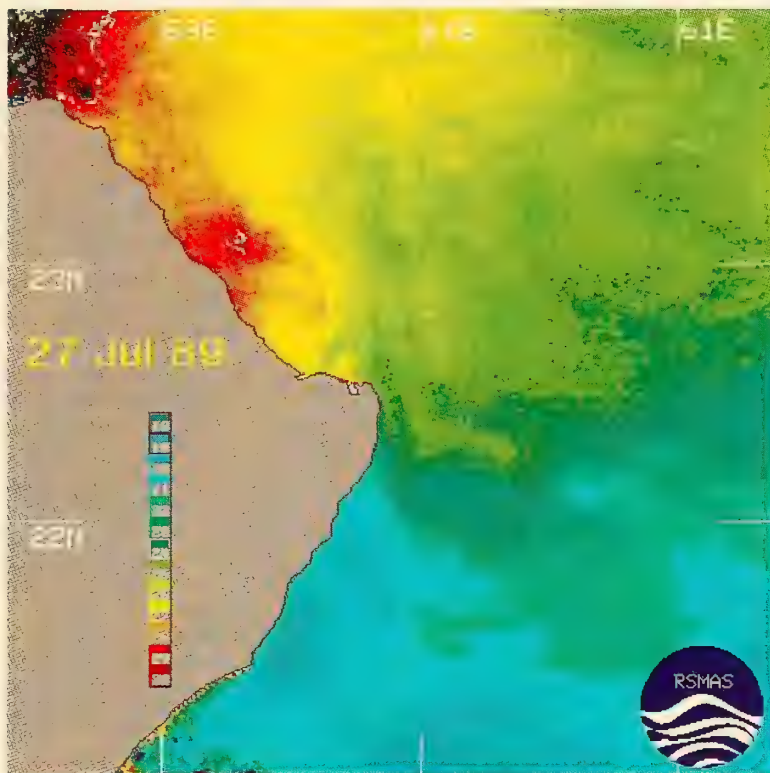


Figure 5. Location of sites surveyed from Ra's Abu Da'ud to Ra's al Hadd, Gulf of Oman. From charts of Muscat and Sur, scale 1:250,000, series 1501, editions 3-GSGS. Director of Military Survey, Ministry of Defence, United Kingdom, 1975.

Excluding periods of high cloud cover, the analysis included 47 days each over Muscat and Masirah in 1988 and 58 and 61 days respectively over Muscat and Masirah in 1989. The total number of images analyzed over the boundary zone was 42 in 1988 and 58 in 1989. Color transparencies were obtained from the SST color images and the positions of thermal fronts and upwelling areas were mapped from these onto acetate film overlays.

(a)



(b)

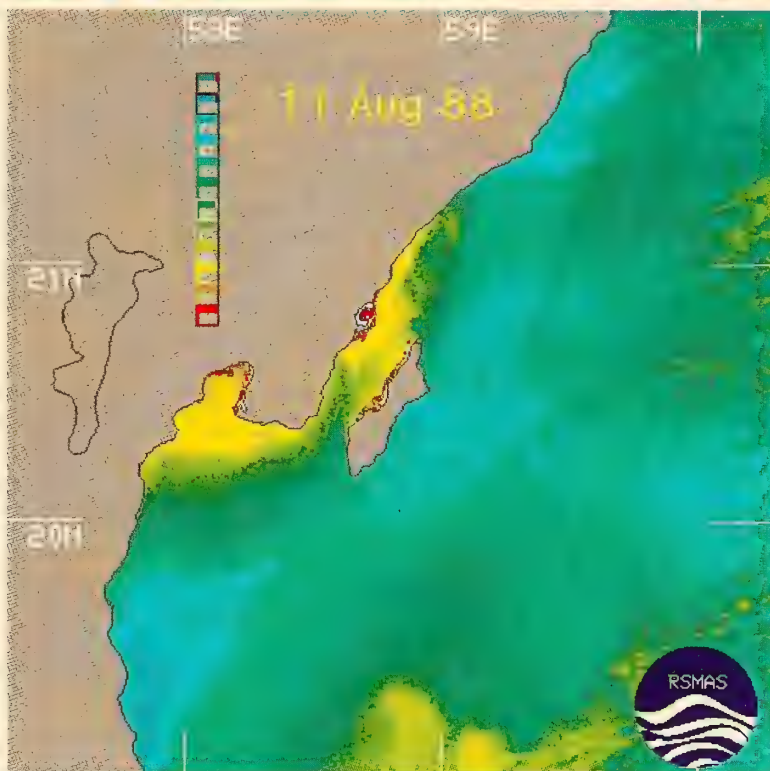


Plate 1. Satellite-derived sea surface temperature (SST) fields off Oman. (a) Easternmost Arabian Peninsula with a marked SST gradient along the Gulf of Oman/Arabian Sea boundary; (b) Masirah Island with high SSTs in Masirah Channel and the northern Gulf of Masirah. An SST scale ($^{\circ}\text{C}$) is provided with each image. [P.W. Glynn]



Figure 6. Location of sites surveyed at Masirah Island, Arabian Sea. From chart of Al Masirah, scale 1:250,000, series 1501, edition 2-GSGS. Director of Military Survey, Ministry of Defence, United Kingdom, 1981.

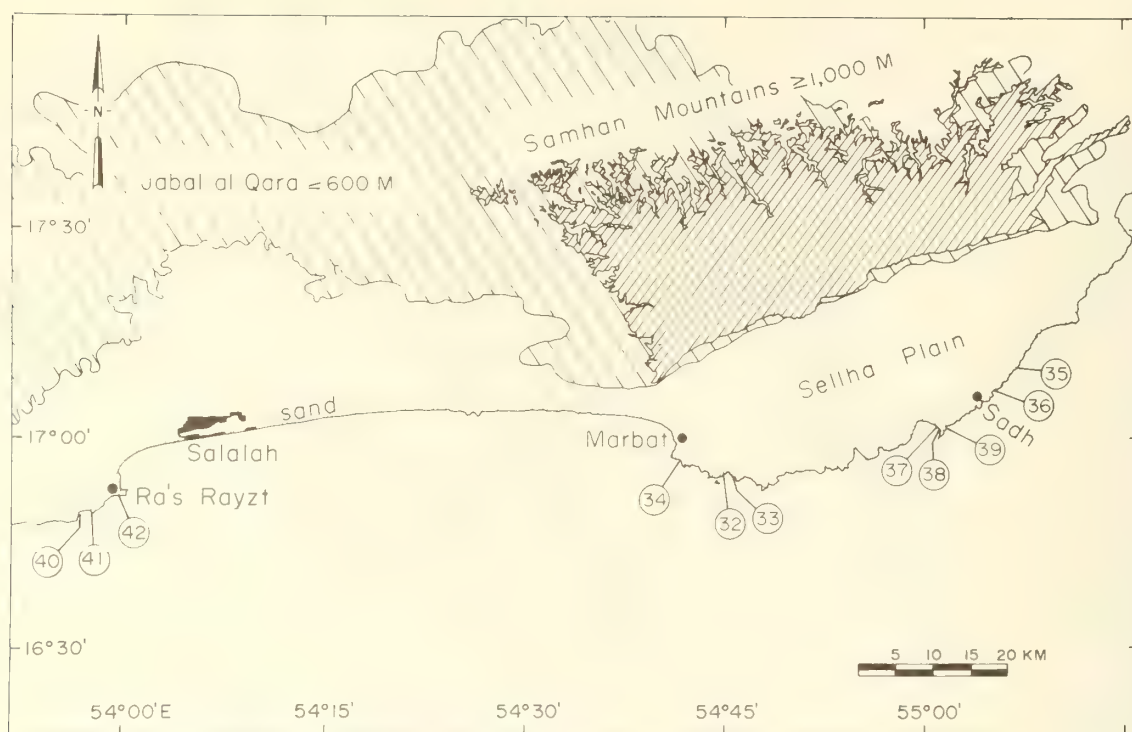


Figure 7. Location of sites surveyed in the Dhofar area, Arabian Sea. Dark patch at Salalah indicates area of high population density. From chart Salala (= Salalah), scale 1:250,000, series 1501, edition 2-GSGS. Director of Military Survey, Ministry of Defence, United Kingdom, 1980. Elevation of al Qara Mountains from Map of Oman, The Sultanate of Oman (2nd ed. revised, 1983), Malt International, P.O. Box 8357, Beirut, Lebanon).

RESULTS

Distribution and Nature of Coral Communities and Coral Reefs

Musandam. Ramose and table *Acropora* species predominated in the areas investigated in the Musandam, although *Pavona*, *Porites*, *Goniopora*, *Montipora*, and *Pocillopora* species also were patchily abundant. The occurrence of coral formations was sporadic, but where present live coral cover tended to be high (often $\geq 60\%$). Zooxanthellate corals ranged in depth from about the extreme low water tidal datum to 10-12 m. Numerous coral species were present at five sites (1, 3, 6, 10 and 11), but no reef development was evident. Reef frame construction, ranging between 2 and 4 m (maximum) in relief, was observed at sites 2, 4, 5, 7, 8, 9 and 12 (Figure 2). A

minimum of 22 reef-building coral species were present at the 12 sites (Table 1).

A small, but well developed fringing reef was present on the east side of the bay at Khasab (site 2). The water was turbid, due to wind-generated waves that suspended fine calcareous sediments, with maximum lateral visibility of 5 m. Massive *Porites* colonies dominated coral cover on the reef flat and from surface views seemed to contribute importantly to reef slope construction as well. The majority of the *Porites* colonies on the reef flat were dead, and these were interspersed with live species of *Platygyra*, *Favia* and *Favites*. Many of the corals on the reef flat were covered with fine sediment. Species of *Acropora*, *Goniopora*, *Platygyra*, and *Stylophora pistillata** were present on the reef slope. A few large (1-2 m diameter) colonies of *Acropora cytherea* were present on the upper reef slope. Corals thinned out at 4 m depth on a gently sloping sand bottom. Maximum relief of this reef was between 3-4 m.

Coral cover was high within the inner reaches of the fjord-like inlets (sites 4-6, 11 and 12) where winds and wave action were reduced and water visibility increased to about 10 m. Fringing reefs were present at sites 4 and 5 with maximum reef frame relief of 2-3 m. The reef flats were only 4-5 m in width and bordered deeply notched (1-2 m), limestone cliffs. The notches were at mid-tidal elevation and presumably formed by lithophagine bioerosion and sand scouring (Cornelius et al., 1973). Corals were distributed sparsely on most reef flats with the following genera observed: *Cyphastrea*, *Favia*, *Favites*, *Goniopora*, *Pavona*, *Platygyra*, and *Porites*. The forereefs in this area exhibited 80-100% cover of *Pavona cactus*, and this coral was abundant from the upper reef slope (2 m) to 10-12 m depth. Some branching *Acropora* species also were present on the upper reef slope.

Coral species richness appeared highest at sites 7-9 (Goat Island or Jazirat el Ghanam). Branching and tabular *Acropora* spp. were abundant (Figures 8 and 9). Several *A. cytherea* colonies 1-1.5 m in diameter were observed at site 7. Some massive *Porites* colonies attained 4 m in height. At site 8, monogeneric thickets of branching *Acropora* spp. formed 1-3 m thick coral frameworks (Figure 8). Also at site 8, virtually monospecific stands of *Pocillopora damicornis* formed reef frameworks that were 3-4 m thick (Figure 9). A few scattered colonies of *Porites solida* were present within the pocilloporid patch reefs. The acroporid and pocilloporid reefs, usually centered between 1 and 5 m depth, covered about 0.5 ha each. *Dendrophyllia*

*The authors of the scientific names of coral species identified in this study are provided in Table 1.



Figure 8. Underwater view of *Acropora* spp. corals, Musandam Peninsula, site 8 (Fig. 2), 4 m depth (21 September 1982).



Figure 9. Underwater view of a dominantly *Pocillopora damicornis* build-up, Musandam Peninsula, site 8 (Fig. 2), 4 m depth (21 September 1982). This patch reef was approximately 0.5 ha and had a maximum reef frame thickness of 3-4 m.

micrantha (Ehrenberg), and other azooxanthellate corals, were abundant on partially shaded limestone boulders at 1-3 m depth. Numerous species of reef corals continued down slope to a sand bottom at 10-12 m depth.

No *Pocillopora* spp. were seen at sites 1-6, but numerous colonies of *P. damicornis* were present in several coral communities at sites 7-12. Several of the latter displayed conspicuous bleached (whitened) branch tips. Occasionally a few colonies of *Pocillopora verrucosa* (Ellis & Solander) with stout branches and distinct verrucae also were found.

Coral communities at sites 7, 9, 11 and 12 appeared to have been subject to repeated rock slide disturbances. Large sections of steep limestone cliffs bordering the shoreline often collapsed, resulting in rock piles that covered the adjacent submarine shelf. Inspection of the undersides of rocks revealed crushed corals. Some of the older blocks were overgrown by corals, indicating successful recolonization and growth following rock slide events.

Schools of herbivorous fishes (e.g., scarids, acanthurids and kyphosids) or large invertebrate predators (e.g., tetraodontids, diodontids and balistids) were conspicuously absent. Large numbers of small predators, e.g. labrids, pomacentrids and haemulids, were abundant (Figures 8 and 9). A few large *Eucidaris metularia* (Lamarck) occasionally were observed on the live branches of *Acropora* corals, but there was no indication that they were feeding on coral tissue. Microfilamentous algae comprised the chief epibenthic plant cover, which are characteristic of reef habitats with reduced herbivory and low nutrient levels (e.g., Hatcher, 1983; Littler and Littler, 1984; Berner, 1990).

Daymaniyat Islands. *Acropora*, *Montipora*, *Pocillopora* and *Porites* species occurred abundantly at most sites in the Daymaniyat Islands (Figure 3). *Acropora cytherea*, 1-2 m diameter colonies, were prominent yet all of these large colonies were dead (Figures 10-13). The majority of these corals were in normal growth position and were overgrown with microfilamentous algae, hydroids, alcyonaceans and bryozoans. *Pocillopora damicornis* often was observed growing on the upper surfaces of dead *A. cytherea* (Figures 10 and 13). Also seen on dead *Acropora* were small (< 30 cm diameter) colonies of *Stylophora* sp., *Porites* sp., *Acropora* sp. and *Symphyllia radians*. The only notable large colonies that still exhibited patches of living tissue were *Porites*, which were tentatively identified as *Porites solida* (Figure 10). Where *Acropora* corals predominated, live cover was low ($\leq 1\%$). Most bottom areas where *Pocillopora* and *Porites* predominated exhibited relatively few dead colonies and showed high live coral cover ($\geq 50\%$, Figure 13). Mixed *Acropora*-*Pocillopora* communities, with nearly all *Acropora* dead and all



Figure 10. Underwater view of a dead, predominantly *Acropora* spp. coral community, Daymaniyat Islands, site 58 (Fig. 3), 4 m depth (20 October 1982). Note live *Pocillopora damicornis* colony resting on top of a dead *Acropora* coral (center of photograph).

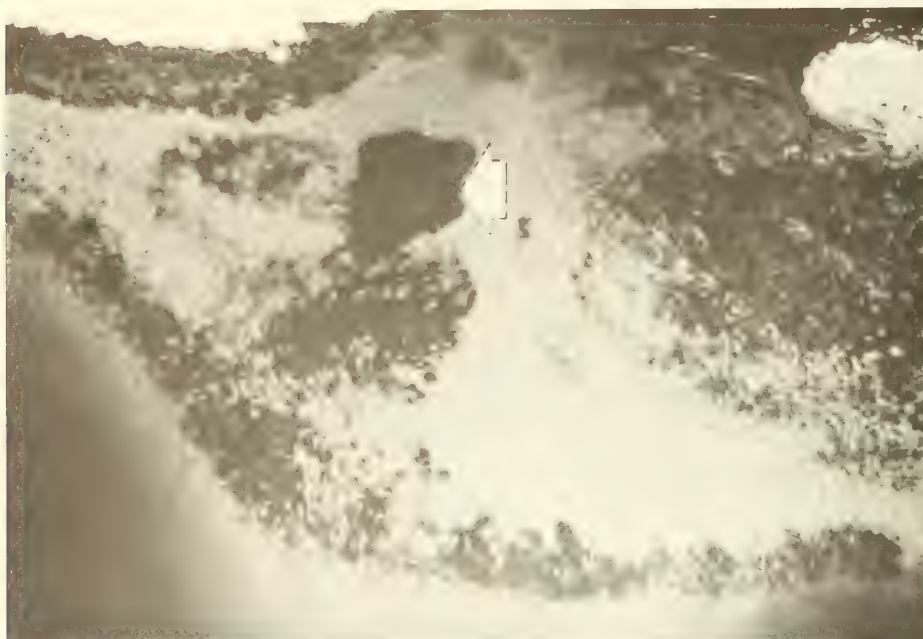


Figure 11. Near-vertical aerial view of leeward side of Jun Island, site 58 (Fig. 3), Daymaniyat group (ca. 600 m elevation, 18 October 1982). Dark, broken patches along shelf edge (bottom) and elsewhere represented mostly dead *Acropora* spp. communities. Dark, solid, trapezoidal patch (arrow) was a live *Pocillopora damicornis* build-up.



Figure 12. Near-vertical aerial view of island east of Jun Island, site 59 (Fig. 3), Daymaniyat group (ca. 600 m elevation, 18 October 1982). Dark patch on shelf edge (arrow) was a live *Pocillopora damicornis* build-up, dark patches on shelf consisted predominantly of dead *Acropora* spp. communities.



Figure 13. Underwater view of live *Pocillopora damicornis* colonies adjacent to dead *Acropora* spp., Daymaniyat Islands, site 60 (Fig. 3), 5 m depth, 19 October 1982. The line of *Pocillopora* colonies in the foreground is overlapping slightly (overgrowing) the dead *Acropora* colonies.

Pocillopora alive, indicated a marked disproportionately higher mortality of acroporid species.

Live corals occurred at a maximum depth of about 15 m, where light levels were high. Underwater visibility was high at all sites, approximately 20 m laterally. Patch and fringing reefs were well developed along the lee (south) sides of the island chain (Figures 11 and 12). Fringing reefs were present at sites 58 and 70. Massive *Porites* sp. were most abundant on the reef flats and shallow sections of these reefs, whereas *Pocillopora damicornis* tended to predominate on the deeper slopes to a calcareous sand bottom at 5-6 m depth. A shallow (1-2 m depth) moat between the leeward reef flat and shoreline was populated with *Platygyra*, *Stylophora*, branching *Porites*, *Montipora*, and *Acropora* at site 58. The framework relief of fringing reefs was approximately 4-5 m.

The dead *Acropora* patch reefs were present at shallow depth (2-5 m). Their vertical framework construction was slight, from about 1 to 3 m only, suggesting a youthful stage of development. These dead reefs, each covering several thousands of square meters of bottom, were observed at sites 58, 60, 63 and 65. *Porites* fringing reefs showed a vertical relief of 4-5 m, and the larger pocilloporid patch reefs appeared to have a relief of 6-7 m. The pocilloporid reefs, virtually monospecific stands of *Pocillopora damicornis*, were present on insular shelves (Figure 11) or at shelf-slope boundaries (Figure 12). Some of the pocilloporid reefs were elongate and paralleled the leeward shelf 4-5 m isobath. Such reefs were well developed at sites 59, 61, 66, 67, 68 and 69. Some pocilloporid reefs were elongate and appeared to follow the 4-5 m isobaths along the shelf edge. The shelf-edge pocilloporid reefs descended gradually into deeper water where they stopped abruptly on a gently sloping calcareous sand plain at 10-12 m depth. The black balistid *Melichthys indicus* Randall & Klausewitz was abundant where holes were present in the deeper sections of pocilloporid reefs.

Although reef building was not observed, coral communities were well developed at sites 57, 62 and 71. Scattered coral knolls constructed by massive *Porites* occurred at site 57. Numerous species occurred at sites 62 and 71 on the north sides of the islands. Wave action there stirred up sediments and reduced lateral visibility to about 10 m. Site 64 was a flat rock bottom with scattered dead coral cover.

Capital area. Nearly all of the reef-building coral species present in the Musandam and Daymaniyat Islands also were found in the Capital area (Figure 4). The chief reef frame builders also were similar in the three regions.

A group of rocky islands located immediately offshore of Ra's as Sawadi, about 85 km west of Muscat on the southern Al Batinah coast, was the location of site 24 (Figure 1). The abundant genera in this turbid (2-5 m lateral visibility) environment were *Acropora*, *Pocillopora* and *Porites*. *Acropora cytherea* and *Platygyra* also were observed. Patch reefs composed of branching *Acropora* and *Pocillopora damicornis* were present around some of the small islands. The maximum depth of these reefs reached only about 8 m, and maximum vertical relief was 1-2 m. A drying reef flat was present on the mainland coast, composed mainly of massive *Porites* colonies.

Pocilloporid reefs were well developed at Fahal Island (site 13) and near Muscat (sites 21 and 22), where they were present in areas relatively sheltered from direct wave assault. Lateral water visibility ranged between 10-20 m during the surveys. These reefs demonstrated high live coral cover (80-100%), were constructed primarily of *Pocillopora damicornis*, and had maximum relief of 6-8 m (Figures 14 and 15). Maximum reef depths ranged between 9-10 m.

The pocilloporid reef on the south side of Fahal Island was at least 1 ha in planar view. The shallowest reef summits, with 100% live coral cover, were 3-4 m below sea level and appeared not to have been exposed at low water. Massive *Porites* sp. colonies, 2-3 m high, were intermingled with *P. damicornis* framework in some areas. The basal margins of some of the *Porites* sp. were overgrown by *P. damicornis*, and a few colonies were nearly completely overtopped by pocilloporid framework. Several large *Diadema setosum* Leske were present at the reef base. The mainland pocilloporid reefs were approximately 0.5 (site 21) and 0.8 (site 22) ha in planar view. The reef flats on both reefs revealed considerable dead coral, mostly in growth position, probably indicative of exposures at low tides. Much of this dead coral was overgrown by crustose coralline algae and microfilamentous algae. This was reflected in the relatively low percent live *Pocillopora* cover on reef flats compared with the seaward slope zone (Figures 16 and 17). Coral species diversity was highest at the reef base at site 21 ($H' = 0.91$), due to the occurrence of species of *Montipora*, *Acropora*, *Goniopora*, *Porites*, *Psammocora*, *Favites*, and *Astreopora* (Figure 16). The highest H' index at site 22 ($H' = 0.77$) was observed on the reef flat, where a few *Acropora* colonies were present (Figure 17). In general, these reefs revealed sparse pocilloporid rubble at the reef base or on adjacent sand plains. Large *D. setosum* were common at the reef base.



Figure 14. Oblique aerial view of the Christian cemetery embayment, site 21 (Fig. 4) (ca. 600 m elevation, 18 October 1982). Dark patch (right of center) is the same pocilloporid patch reef shown in Fig. 15. Other linear patches skirting the shoreline are incipient fringing reefs composed of a variety of coral species.



Figure 15. Underwater view of fringing pocilloporid reef, Capital area, near Christian cemetery, site 21 (Fig. 4), 2 m depth, 15 October 1982. A school of the Arabian Butterflyfish, *Chaetodon melapterus*, is visible in the foreground feeding on live *Pocillopora damicornis*.

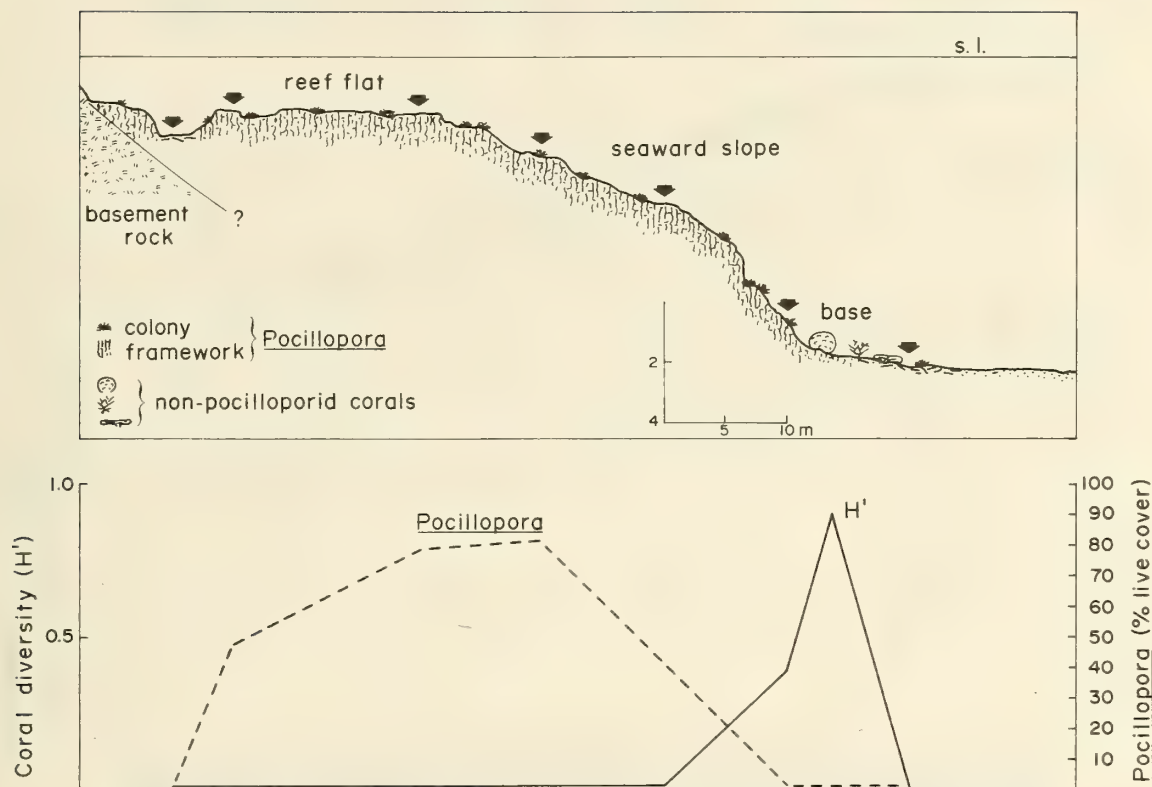


Figure 16. Cross-section sketch of a pocilloporid reef near the Christian cemetery (site 21, Fig. 4) from shoreline to off-reef sand plain (above). Sampling areas across the reef are denoted by arrows, and the corresponding percent live *Pocillopora damicornis* cover and coral species diversity (H') are indicated on the graph (below). S.l. is approximately mean sea level. Data from chain transect sampling performed on 15 October 1982.

Chaetodon melapterus Guichenot, the Arabian Butterflyfish, often was observed feeding on live *P. damicornis* colonies on mainland pocilloporid reefs (Figure 15). They appeared to be removing polyps as do other butterflyfishes in different areas of the Pacific Ocean (Hourigan et al., 1988). Only two porcupinefish, *Diodon hystrix* Linnaeus, were seen during the entire survey (at site 21). Several other fishes that commonly frequented pocilloporid reefs included: unidentified benthic pomacentrids and schools of *Abudefduf saxatilis* (Linnaeus) (Pomacentridae); *Cephalopholis miniatus* (Forsskal) and *Cephalopholis argus* Bloch & Schneider (Serranidae); *Ostracion tuberculatus* Linnaeus (Ostraciontidae); *Rhineacanthus aculeatus* (Linnaeus) (Balistidae); *Zebrasoma xanthurum* (Blyth) (Acanthuridae); *Carangoides fulvoguttatus* (Forsskal) (Carangidae); *Heniochus acuminatus*

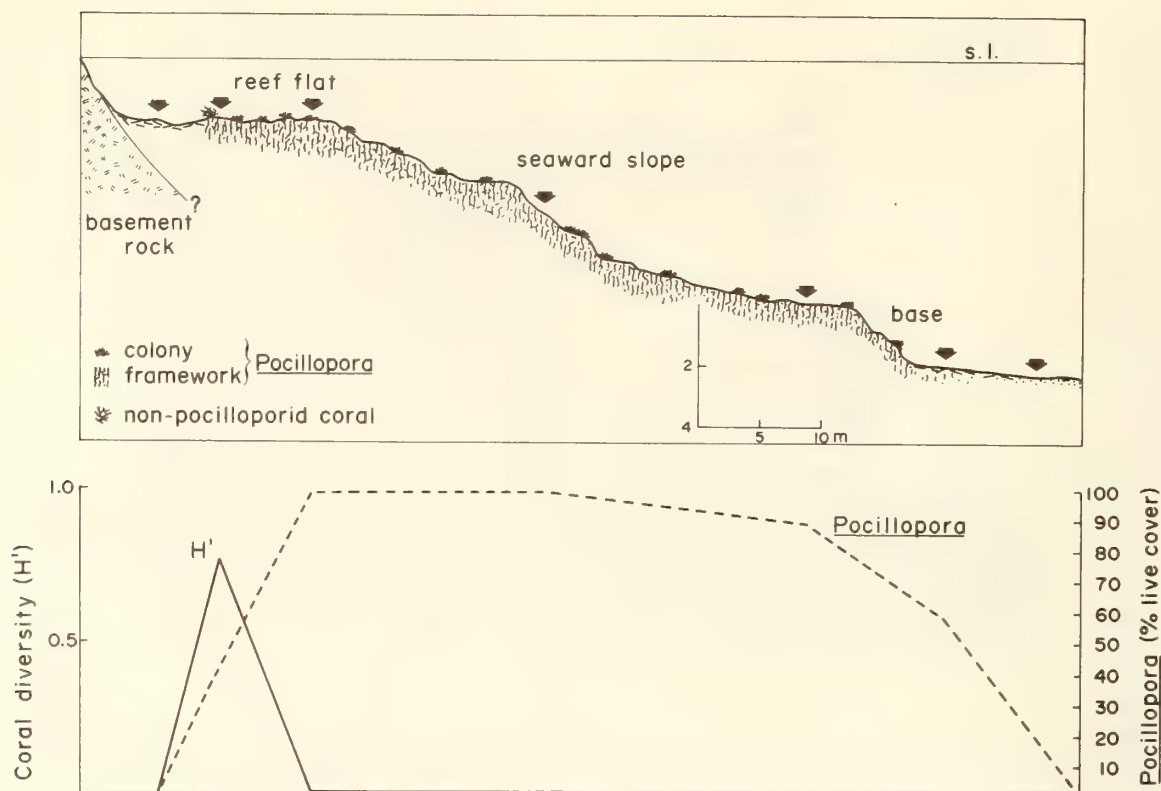


Figure 17. Cross-section sketch of a pocilloporid reef off Jazirat Muscat near the Sultan's Palace (site 22, Fig. 4) from shoreline to off-reef sand plain (above). Sampling areas across the reef are denoted by arrows, and the corresponding percent live *Pocillopora damicornis* cover and coral species diversity (H') are indicated on the graph (below). S.l. is approximately mean sea level. Data from quarter meter quadrat sampling performed on 24 October 1982.

(Linnaeus) (Chaetodontidae). However, large schools of herbivores (e.g., parrotfishes, acanthurids, kyphosids) were not seen.

Small patches (5 X 20 and 10 X 20 m) of live *P. damicornis* were present at Bandar Khayran (site 16). These patches were thin with maximum vertical buildups of 1-2 m. Two dead pocilloporid formations were observed at Bandar Jissah. The larger of these (site 19, between north island and the mainland, see Map 1 in Salm, 1985), about 0.8 ha and 3-4 m high, was broken apart with coral rubble widely scattered. Large sections of this reef were overgrown with microfilamentous and macroalgae, and alcyonaceans. The second dead pocilloporid patch (site 74, south side of island in the central branch of the main bay, Salm, 1985) was in growth

position. Another dead pocilloporid formation, observed by B. Speck (pers. comm.) in a bay to the south of Bandar Khayran, was not visited during this study.

Small *Acropora* patch reefs, usually with a maximum vertical buildup of 1-2 m, were observed immediately west of Qantab (site 14), inside Bandar Khayran (site 16), and in the central branch of the main bay at Bandar Jissah (site 17). Lateral water visibility was about 10 m at these sites. *Acropora cytherea*, with larger colonies 2-2.5 m in diameter, predominated at sites 14 and 17. Most of these corals were dead with several colonies observed being eaten by *Acanthaster planci* (Figure 18). *Goniopora* sp., about 1 m diameter colonies, were also present and did not show signs of predation by *Acanthaster*. *Acropora* thickets, with up to 100% live cover of branching species, were present at site 16.

Coral reefs with other than acroporid and pocilloporid species predominant were seen at four sites. A fringing reef composed of numerous



Figure 18. Underwater view of *Acanthaster planci* resting on a tabular colony of *Acropora cytherea*, 5 m depth, Bandar Jissah, site 17 (Fig. 4), 15 October 1982. Approximately one-third of this 1.5 m diameter colony had been eaten by the three *Acanthaster* present between the tabular branches.

genera, e.g. *Stylophora*, *Pocillopora*, *Acropora*, *Goniopora*, *Porites* and *Pavona*, extended along the western shore of the large island at Bandar Khayran (site 15). This reef displayed a vertical buildup of 2-3 m, but the framework ended abruptly at 5-6 m depth. Several aggregations of *Diadema*, with 25 to 50 individuals each, were present at the reef base. Thickets of branching *Montipora* sp. covered 10s of square meters inside Bandar Khayran at site 16. A *Porites* sp. fringing reef was developed in turbid water (1-2 m lateral visibility) at Khawr Yenkit (site 18). This reef had a relief of 2-5 m. Most of the coral was dead at 1 m depth. A small, monospecific *Goniopora* sp. patch reef was present in a sheltered cove at site 23. This reef covered a 50 X 20 m area, exhibited 100% live cover, and had a maximum reef frame relief of 3-4 m.

No reef development was observed at sites 20, 56, 72, 74 and 75. However, species rich coral communities characterized sites 56, 74 and 75, all of which were subject to different levels of *Acanthaster* predation. The most abundant genera at site 56 were *Pocillopora*, *Stylophora*, *Porites* (including both dendritic and massive species), and an encrusting *Montipora* sp. *Acropora* were predominant at site 74, and *Pocillopora* and *Porites* at site 75.

Ra's Abu Da'ud to Ra's al Hadd. Lateral water visibility was only 3-6 m at sites 25-31 (3-4 October 1982). Plankton blooms were evident at most sites, including large numbers of brown, stinging jellyfish. Few corals were seen at sites 25-27, northwest of Sur (Figure 5). Species belonging to the genera *Pocillopora*, *Stylophora*, *Acropora*, *Porites* and *Platygyra* were observed scattered on cobbles and boulders at site 25.

A small patch reef was present just inside the west bay entrance at Khor al Hair (site 28). This reef was only 2-3 m deep, and was constructed dominantly of massive *Porites* and, to a lesser degree, *Goniopora*. Alcyonaceans dominated sites 29-31. A few corals belonging to the genera *Pocillopora*, *Stylophora*, *Acropora*, *Porites*, *Goniopora* and *Platygyra* also were seen. Large encrusting alcyonacean colonies were observed overgrowing and killing some of these corals (Figure 19).

Environmental conditions changed dramatically at Ra's Abu Da'ud with clear water (10-12 m visibility) and well developed coral communities prevalent, similar to those reported in the Capital area. *Pocillopora damicornis* reef building was evident in two areas between an island and the mainland shore. Maximum framework development ranged between 1-3 m. Both of the pocilloporid reefs contained large dead sections with surfaces that appeared to have been planed. These leveled surfaces were colonized mostly by *Acropora* spp. and *P. damicornis*, but small colonies of *Stylophora*,



Figure 19. Underwater view of 'soft corals' (alcyonaceans) in the process of spreading over the substratum and overtopping reef corals, including *Goniopora* sp., 4 m depth, east of Sur, site 30 (Fig. 5), 4 October 1982.

Montipora and *Platygyra* also were present. *P. damicornis* dominated large sections of the dead reef frame with 100% live cover. In other areas, *Acropora* spp. were predominant with many examples observed of branching and table *Acropora* overtopping *Pocillopora* and *Stylophora*. Some 20-30 cm diameter pocilloporid colonies were underneath and completely shaded by the acroporids.

Masirah Island. Reef corals were abundant at Masirah Island and the best developed coral communities were found along the northwestern coast (Figure 6). *Pocillopora damicornis* and *Montipora foliosa* were among the more abundant species with the following genera also well represented at several sites: *Stylophora*, *Porites*, *Favia*, *Favites*, *Leptoria*, *Platygyra*, and *Acanthastrea*. Relatively few *Acropora* spp. were seen at Masirah compared with the Musandam, Daymaniyat Islands and Capital area. The water was highly turbid, with 1-3 m visibility, at most sites. This was caused by SW winds that continued for several days (maximum velocity 7 knots during site visit), and wave action over the shallow shelf, which resuspended fine carbonate sediments.

Few corals were present at sites 43 and 44, which were inhabited more by macroalgae (e.g., *Padina* and *Caulerpa*) and zoanthids (*Palythoa*). While a species rich coral community was found at site 45, most of this patch that is designated as a coral bottom on the nautical chart (Figure 6) contains few corals. On the west side of Masirah, corals also were sporadically abundant at sites 47, 48 and 55, but seagrasses and macroalgae (e.g., *Caulerpa* and *Sargassum*) predominated.

Fringing coral reefs dominated the coastline from site 49 north to site 54, including sites 46, 50 and 51 (Figure 6). These reefs were shallow, ranging between 1.5-5 m depth, with maximum vertical framework relief of 3-4 m. *Pocillopora damicornis* and *Montipora foliosa*, either alone or together, were the chief reef-building species (Figure 20). *Acropora* reefs were not observed at Masirah Island as erroneously attributed by Sheppard et al. (1992) to Glynn (1983a). On reef exposures where internal structures were visible, *P. damicornis* contributed disproportionately to the framework with mostly live colonies of *M. foliosa* populating the dead pocilloporid framework at the surface. *M. foliosa* contributed predominantly to the live

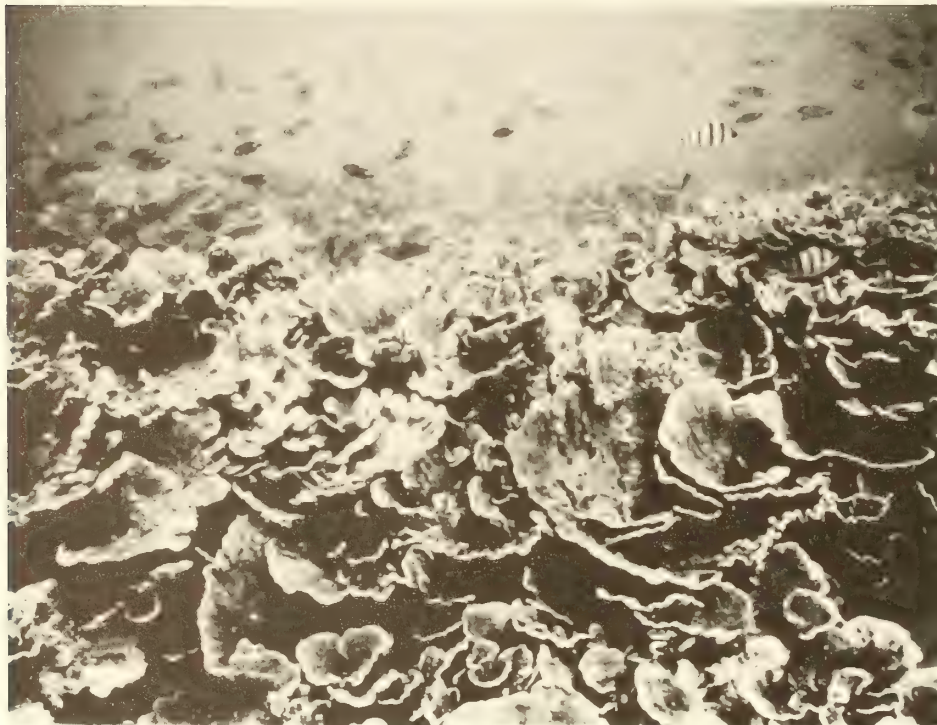


Figure 20. Underwater view of live *Montipora foliosa* buildup, incipient fringing reef, 3 m depth, Masirah Island, site 54 (Fig. 6), 12 October 1982.

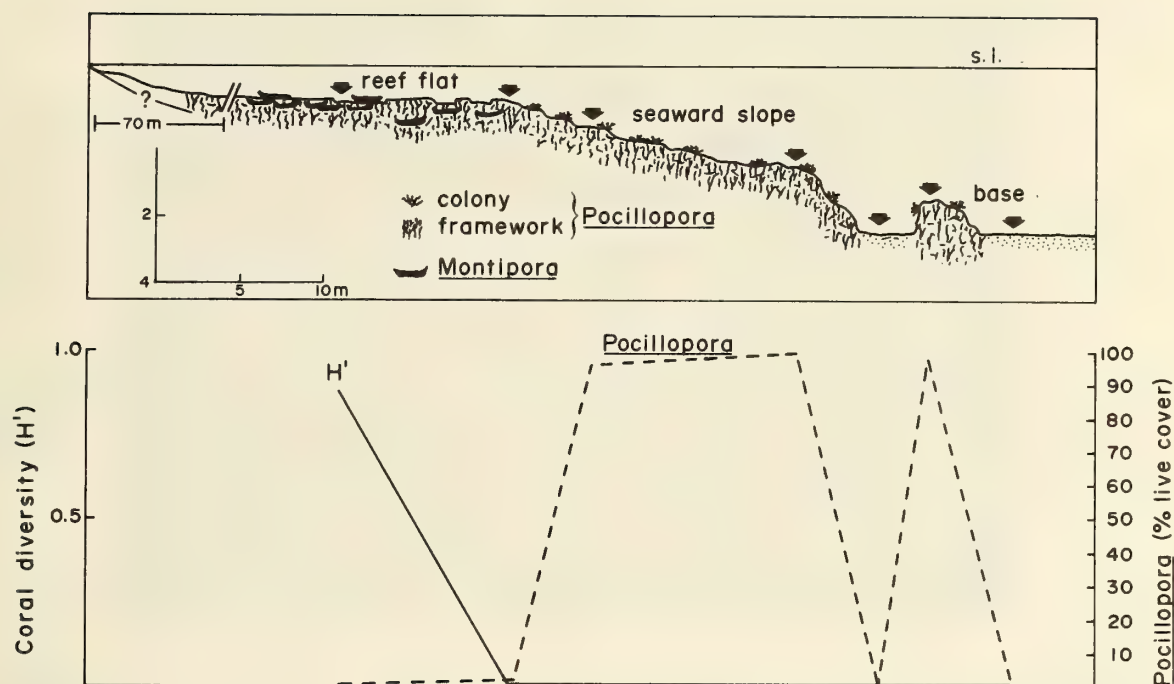


Figure 21. Cross-section sketch of a dominantly pocilloporid reef off the west side of Masirah Island (site 46, Fig. 6) from shoreline to off-reef sand plain (above). Sampling areas across the reef are denoted by arrows, and the corresponding percent live *Pocillopora damicornis* cover and coral species diversity (H') are indicated on the graph (below). S.l. is approximately mean sea level. Data from quarter meter quadrat sampling performed on 12 October 1982.

cover at sites 49, 50 and 51. At sites 46 and 54, *P. damicornis* also was abundant, especially on the seaward slope (Figure 21). Other coral genera (e.g., *Stylophora*, *Acropora*, *Cyphastrea*, *Favia*, *Favites*, and *Acanthastrea*) were largely restricted to reef flats where pocilloporid and montiporid cover was low. The reef flats in this area are exposed during extreme low water (M.A. Al-Barwani, pers. comm.). Large numbers of rock scallops were attached between the basal branches of live *Pocillopora* in the slope zone at site 50 (Figure 6). The reef framework abruptly ended in a thick carbonate sand bottom with few live, intact corals or broken fragments and rubble at the reef base (Figure 21).

Chaetodon melapterus were observed on most fringing reefs and were seen feeding on live *Montipora foliosa*, although it could not be determined what the butterflyfish were feeding on (e.g. mucus, coral tissues). Schools of

large fish grazers or large invertebrate predators were not observed at Masirah Island.

At site 55, *Sargassum* spp. occurred as dense beds at 0.5-1 m depth, with 1-1.5 m long blades forming a thick canopy. Numerous scattered corals were attached to the dead coral boulders beneath the canopy, including *Psammocora*, *Stylophora*, *Montipora*, *Goniopora*, *Porites*, *Cyphastrea*, *Favia*, *Favites*, *Galaxea*, *Acanthastrea*, and *Turbinaria*. At 1.5-2 m depth, between 100-200 m from the shoreline, the mixed macroalgal/coral community was replaced by crustose coralline algae, which were growing on a thin (0.5-1 m) framework of *Montipora*. This fringing reef was only sparsely populated by corals, chiefly *Montipora foliosa*. Farther seaward the unbroken fringing reef became separated into isolated blocks, which eventually thinned out and disappeared.

Coral communities intermixed with macroalgae and seagrasses were observed at sites 47 and 48. Among the common genera observed were *Stylophora*, *Montipora*, *Porites*, *Favia*, *Favites*, *Leptoria*, *Platygyra* and *Acanthastrea*. The summits of many large colonies of the massive genera (e.g., *Porites*, *Leptoria*, and *Platygyra*) were partially covered with carbonate sand. SST and water visibility decreased markedly around the north end of Masirah, from site 53 to site 52. Only scattered colonies of *Stylophora pistillata* were observed at site 53 and *Favia* and *Favites* at site 52. Macroalgae were predominant at these sites.

Dhofar. The rocky coast from Marbat to slightly east of Sadh was populated with lush communities of frondose macroalgae (Figure 7). Species of Sargassaceae (Phaeophyta) were especially abundant, their buoyant blades forming a canopy with a dampening effect on approaching swells. Other abundant brown algae included *Bifurcaria* sp., *Cystoseira* sp., the kelp *Ecklonia radiata* (C. Ag.) J. Agardh, *Padina* sp. and *Turbinaria* sp. The red alga *Hypnea musciformis* (Wulfen) (Rhodophyta) also was abundant along with the green algae *Caulerpa* spp. and *Ulva* sp. (Chlorophyta). For more information on the algal communities and rocky shore fauna in this area, consult IUCN/ROPME/UNEP (1984).

Water visibility was only 3-5 m at sites 32-34 near Marbat. Macroalgal cover was near 100% from the mid-intertidal zone to 3-5 m depth. Associated with the algae were abalones (*Haliotis mariae* Wood), sea urchins (*Echinometra*, *Stomopneustes*, *Echinostrephus*) and unidentified starfish. Only a few corals were seen shallower than 5 m (Figure 22). Corals increased in abundance between 5 and 10 m with a concomitant decrease in macroalgal cover. Most colonies were small. However, some large colonies



Figure 22. Underwater view of macroalgae surrounding a reef-building coral (*Platygyra*, center), 3 m depth, east of Marbat, site 32 (Fig. 7), 6 October 1982.

were present including species from the genera *Acropora* (40 cm diameter tables), *Astreopora* (80 cm diameter), *Porites* (35 cm high massive colonies), *Favites* (50-60 cm, longest dimension), and *Turbinaria* (75 cm diameter). *Stylophora pistillata* was common, but *Pocillopora* was rarely seen.

The water conditions and shallow marine community composition near Sath (sites 35-39) were similar to those at Marbat. Quantitative sampling of the epibenthos to 11 m depth (sites 35 and 39) revealed primarily macroalgal communities. At site 35, *Ulva* was the predominant alga with occasional *Sargassum* plants also present. Both crustose and articulate coralline algae were often present under the macroalgal canopy. Corals (*Acropora* and *Stylophora*) occurred only between 8 and 11 m depth. *Sargassum* spp. were the most abundant macroalgae at site 39. Corals were more common below 5 m with *Acropora*, *Favites* and *Cyphastrea* present to 11 m depth.

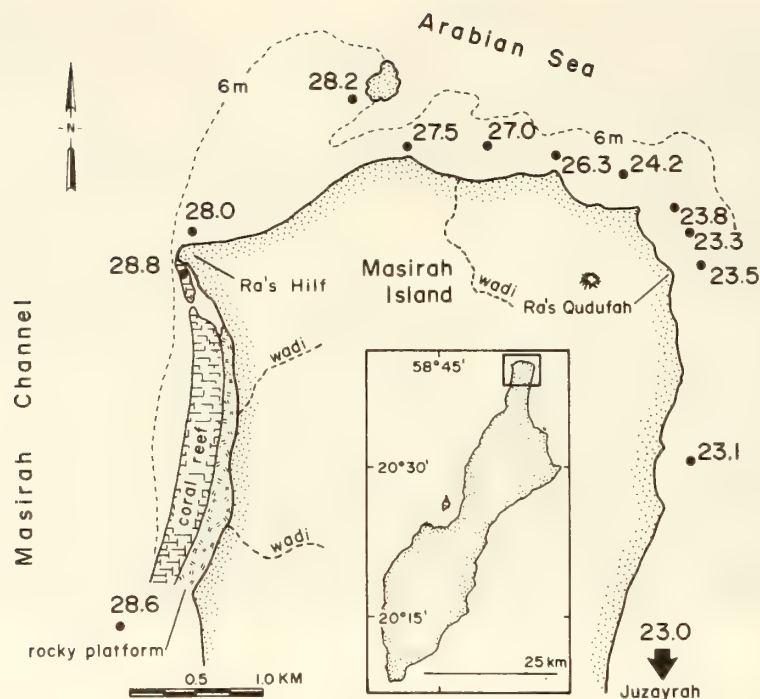


Figure 23. SST ($^{\circ}\text{C}$) gradient around the north end of Masirah Island. Measured between 0850-1140, 12 October 1982. The southernmost temperature was measured at Juzayrah, about 15 km south of Ra's Qudufah. Base map from Everts et al. (1983).

Thermal Environments and Seasonal Variations

Shore-based sea temperature observations (1982). Sea water temperatures were measured at various sites on the Arabian Sea coast during a transitional warming period following the 1982 SW monsoon season. SSTs ranged between 28.2°C and 30.8°C (10-12 October) at all sites on the west side of Masirah Island. The high temperature (30.8°C) was measured nearshore at Qa' ad Kalban (site 55) at 1415; 20 m offshore SST was 28.8°C at 1422.

A well defined thermal front was evident along the north end of Masirah (Figure 23). SST was 28.8°C over a fringing reef off the NW corner of the island. A steady decline in SST occurred around the north end of the island with a 3°C difference (26.3°C - 23.3°C) evident over a 1.2 km stretch off the NE corner of the island. The lowest SST (23.0°C) was observed at Juzayrah Island (site 52), about 12 km south of Ra's Qudufah.

SSTs observed off the Dhofar coast (6-9 October) generally were similar to those reported for the east coast of Masirah. Relatively high SSTs occurred nearshore at two sites between Marbat and Sath: 27.0°C (site 32) and 25.0°C (site 37). These temperatures, measured in bays in the late morning and early afternoon, probably reflect some surface warming that occurred in areas with heavy macroalgal canopies. The bottom (4 m) temperature at site 32 was 24.5°C. SSTs offshore (about 1 km) of site 37 ranged between 22.8° and 24.0°C. The lowest nearshore temperatures occurred at site 35, where SST was 22.5°C; 22.0°C was recorded at 8 m depth. SSTs were somewhat higher west of Ra's Rayzt with nearshore temperatures that ranged between 25.5°-26.7°C.

Nansen cast data (1933-1979). To amplify the temperature records obtained in 1982, a long-term data base from Nansen casts was analyzed for geographic and seasonal trends. During the NW monsoon (December-February), characterized by onshore water movement and downwelling along the Arabian Sea coast, SSTs are relatively high (24°-25°C) (Figure 24). SSTs are low in the Gulf of Oman in the winter season and high in the summer (Figure 24). In contrast, summer SW monsoon SSTs were low along the Arabian Sea coast, a reflection of strong upwelling in this season (Figure 25).

SST isotherm plots along the Arabian Sea coast of southern Oman similarly reveal relatively warm conditions during the NW monsoon (Figure 26) and cool upwelling conditions during the SW monsoon (Figure 27). A strong SST gradient (19°-23°C) is evident along the SE side of Masirah Island in July with the lowest temperatures nearshore. Lower SST isotherms (21°-22°C) also are closest to coastal areas near Marbat, suggesting that active upwelling occurs very close to shore and/or upwelled water is preferentially retained there.

The synoptic seasonal variations in SST illustrate well the contrasting thermal environments in the Gulf of Oman and Arabian Sea (Figure 28). In both regions, SST increases from March through June with maximum annual mean temperatures in June. Notably high extreme SSTs of 36°-37°C occurred in June in both regions. In the Gulf of Oman, mean SST remains high (30°-31°C) through September and then decreases through February. Monsoon-induced upwelling in the Arabian Sea causes summer temperatures to fall suddenly in July with mean SST remaining relatively low (24°-25°C) through September. A 2 month post-monsoon increase in SST occurs in the autumn, to be followed by lower mean temperatures from December through February. Extreme low SSTs were nearly 2°C lower in the Arabian Sea (July) than in the Gulf of Oman (February).

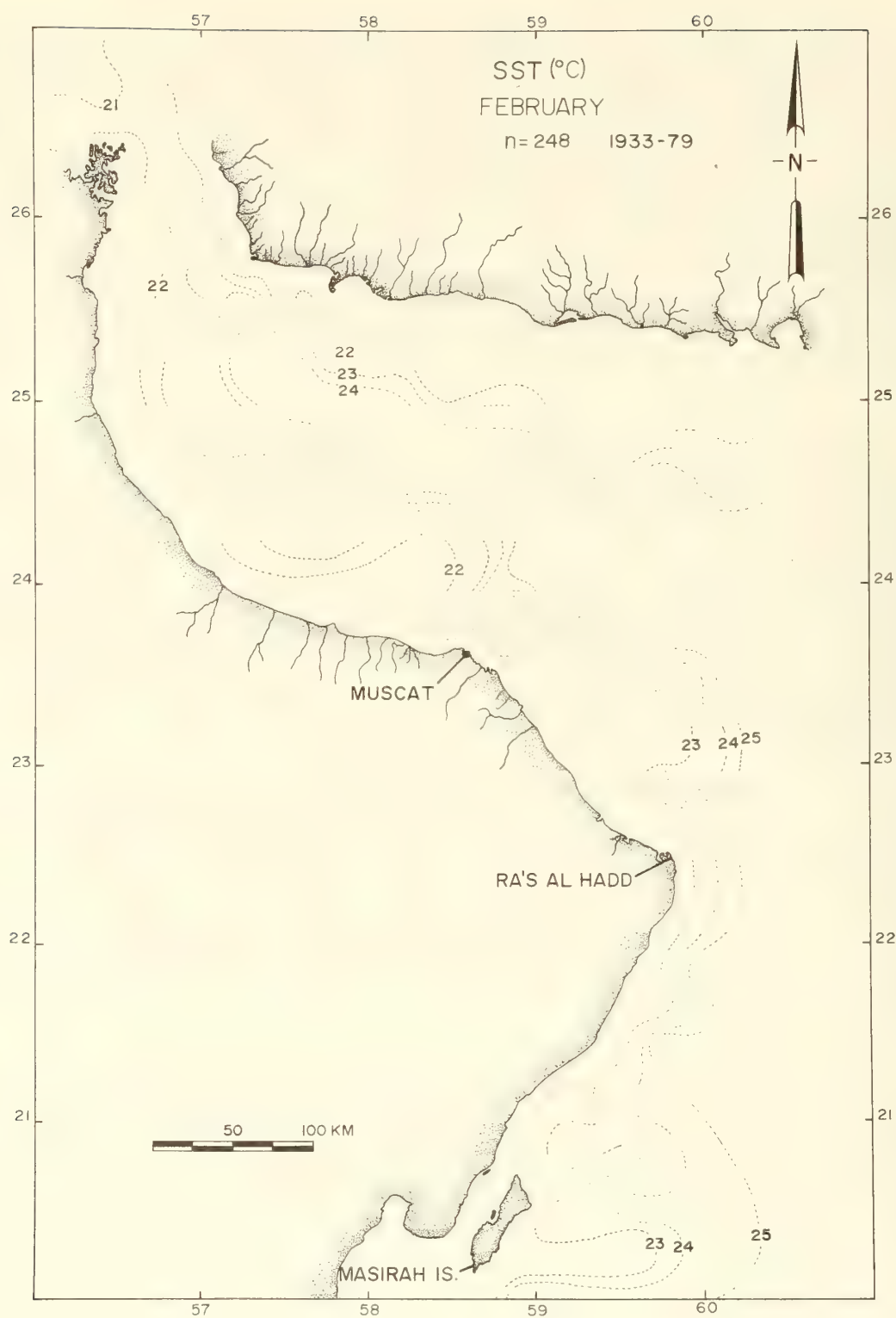


Figure 24. Mean monthly isotherms constructed from Nansen cast data from Gulf of Oman and Arabian Sea waters, northern region of Oman, February (1933-1979).

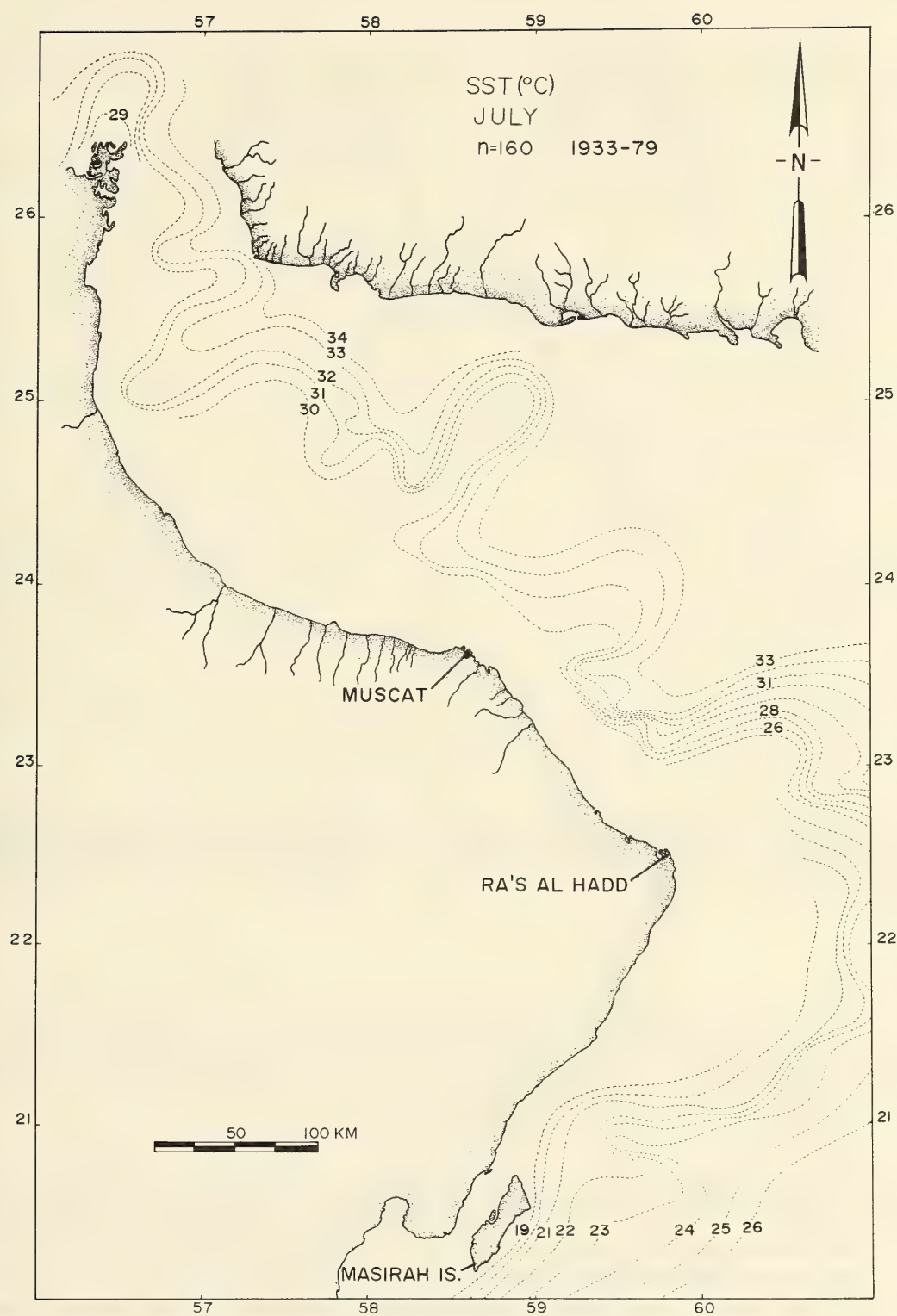


Figure 25. Mean monthly SST isotherms constructed from Nansen cast data from Gulf of Oman and Arabian Sea waters, northern region of Oman, July (1933-1979).

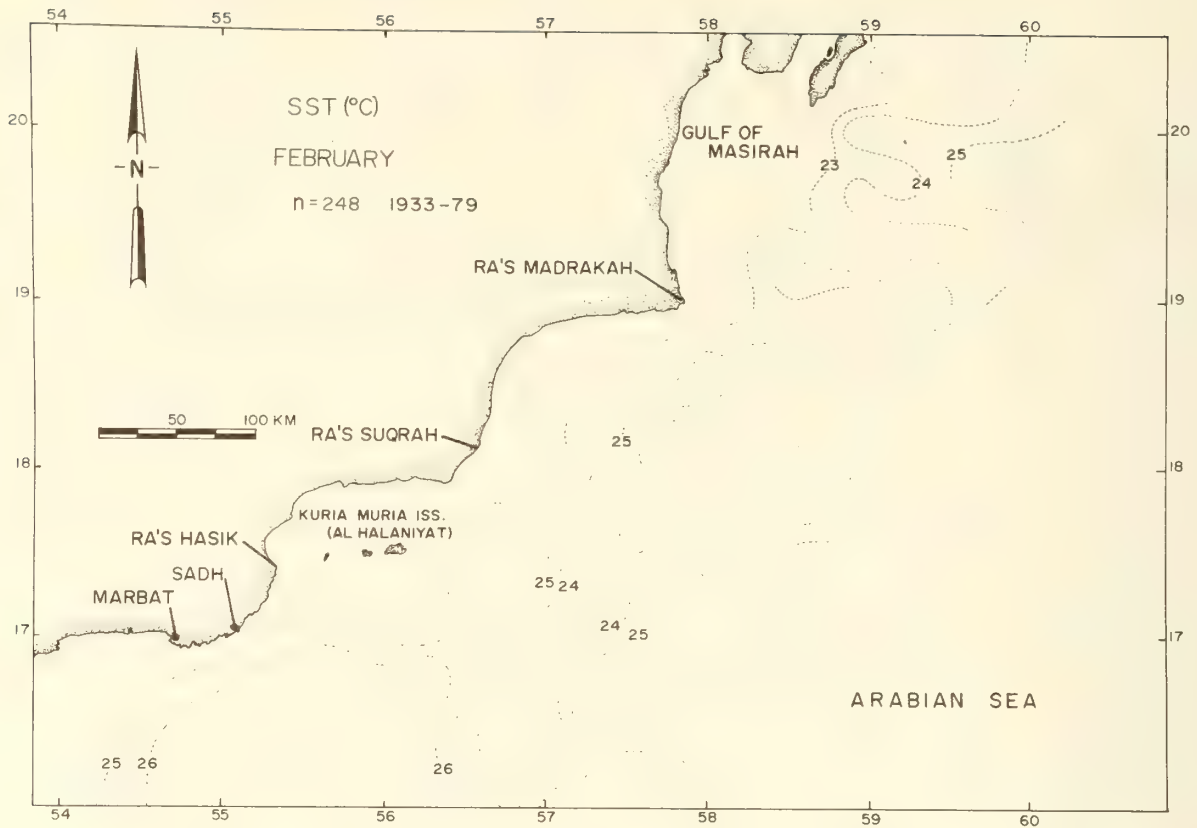


Figure 26. Mean monthly SST isotherms constructed from Nansen cast data from Arabian Sea waters, southern region of Oman, February (1933-1979), NE monsoon.

Because the Nansen cast measurements typically were made in shipping lanes, these data did not reveal information on nearshore temperature structures that influence coral communities.

Remote sensing data (1988, 1989). Analysis of SST fields from satellite imagery provided details of nearshore temperature conditions and variations during the SW monsoon. The grids analyzed are shown in Figure 29. The images in Plate 1 reveal a thermal front off Ra's al Hadd in July 1989 (a), and warm pools on the NW side of Masirah Island and at Barr al Hikman, across Masirah Channel on the mainland coast, in August 1988 (b). SSTs on the south side of Ra's al Hadd were 24°-25°C, and increased to 27°-28°C around the point towards the NW (near Sur). The temperature change was more abrupt at Masirah Island, with SSTs of 23°-24°C at easterly exposures and 27°-28°C towards the west.

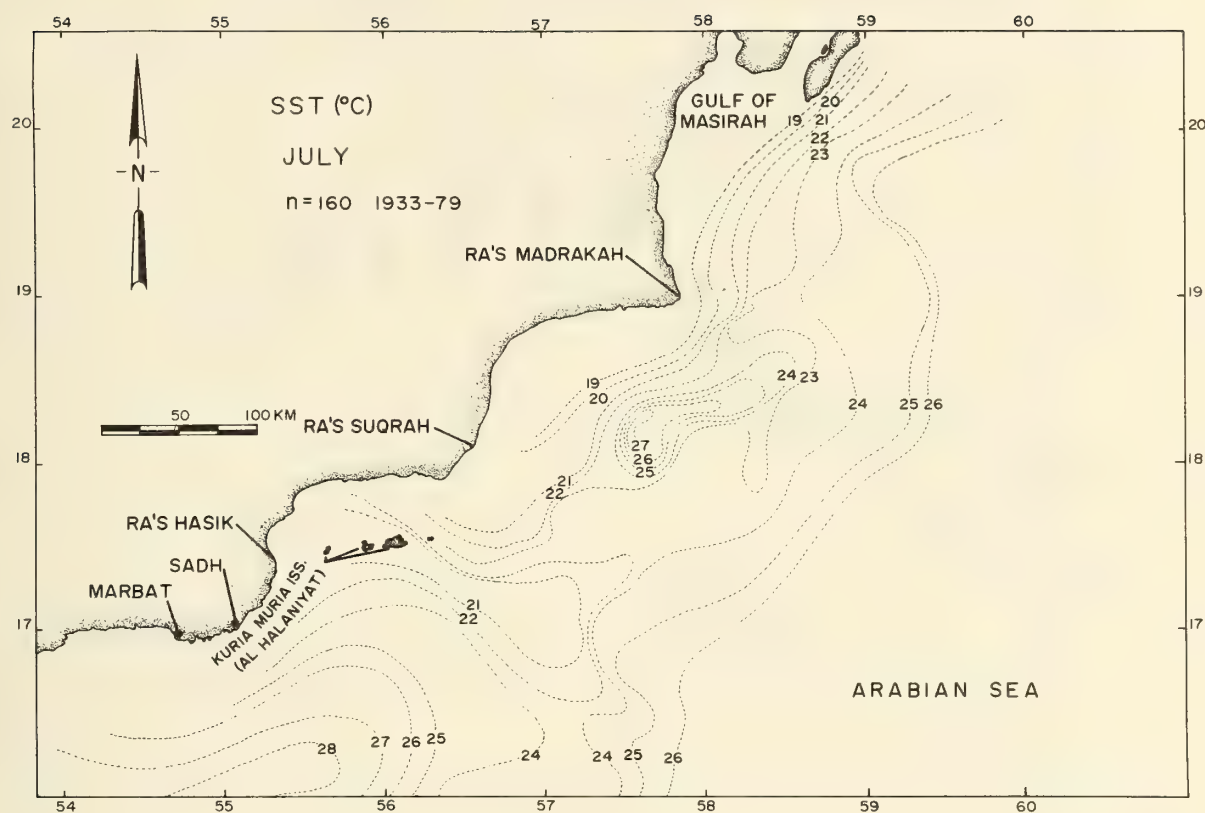


Figure 27. Mean monthly SST isotherms constructed from Nansen cast data from Arabian Sea waters, southern region of Oman, July (1933-1979), SW monsoon.

The Muscat and Masirah Island areas are compared in Figure 30 in terms of seasonal upwelling activity and persistence of the warm pool respectively. Only a single, weak upwelling plume was detected off Muscat in 1988 (Figure 30 A), in early July, whereas large areas experienced upwelling in 1989, most notably in August and September (Figure 30 B). Warm pools covered extensive areas along the west side of Masirah Island and at Barr al Hikman in 1988 (Figure 30 A; Plate 1). The mean area of the warm pool in 1988 was 1,001 square nautical miles ($= 1,855 \text{ km}^2$). Warming was not as evident in 1989 (Figure 30 B); the warm pool then had a mean area of only 738 square nautical miles ($= 1,368 \text{ km}^2$).

The seasonal advection of cool, upwelled waters into the SW sector of the Gulf of Oman is indicated in Figure 31 for 1988 and 1989. In both years, the onset of cooling began in late May. Coastal cooling began as early as June-July in 1989, but not until August in 1988. The penetration of cool,

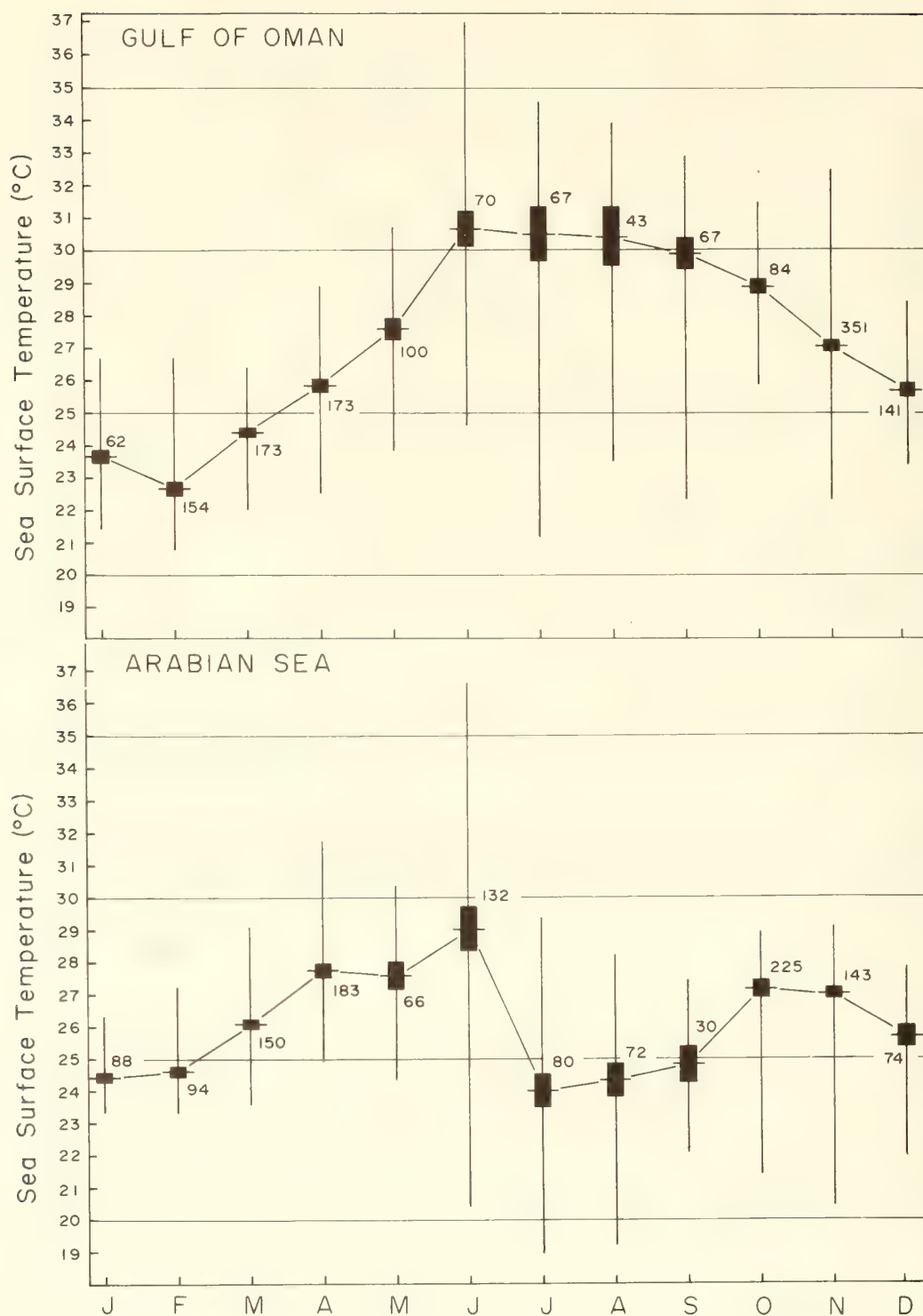


Figure 28. Seasonal SST variations in the Gulf of Oman (above) and Arabian Sea (below) constructed from Nansen cast data, 1933-1979. Horizontal lines denote monthly mean values, bars the 95% confidence intervals of means and vertical lines the maximum and minimum temperatures. Numbers of observations are indicated for each month.

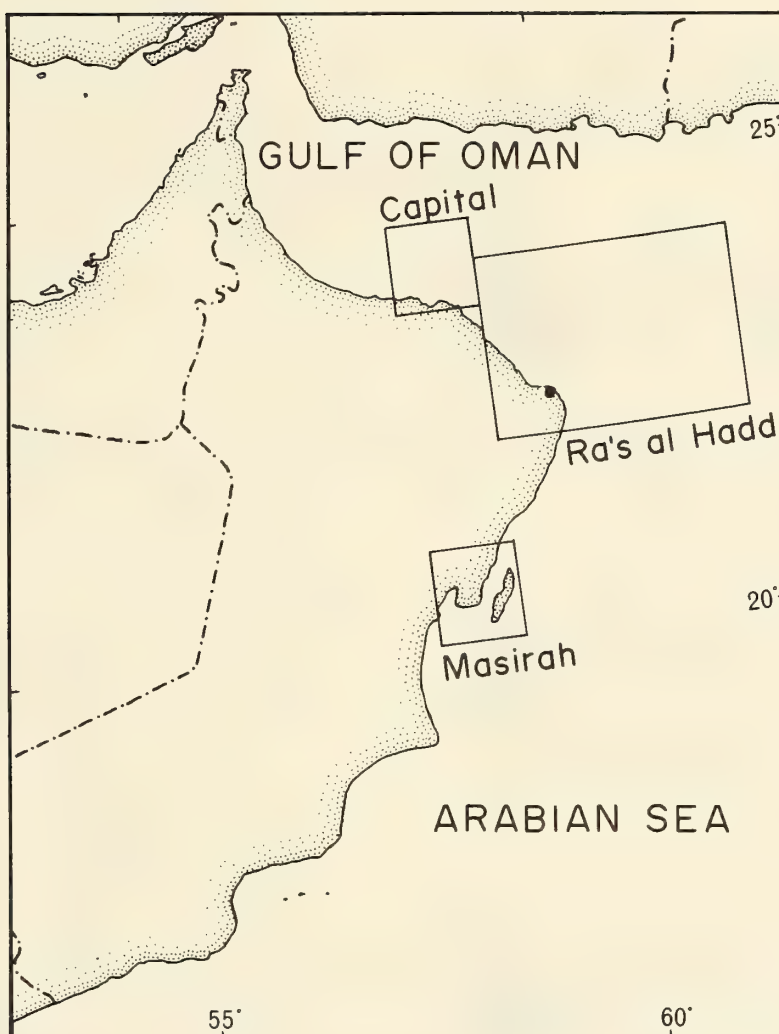


Figure 29. Areas studied for SST patterns from 1988 and 1989 (satellite infra-red data). Location of 1° grids over the Muscat-Daymaniyat Islands (Capital) and Masirah Island areas, and the 6° grid over the Gulf of Oman-Arabian Sea boundary off Ra's al Hadd.

upwelled water from the Arabian Sea into the Gulf of Oman was greater in 1989 than in 1988, and the cool front off Ra's al Hadd persisted 2-3 weeks longer in 1989 than in 1988. Synoptic plots illustrating the percentage occupancy of cool fronts also reveal a greater spatial penetration into the Gulf of Oman in 1989 compared with 1988 (Figure 32).

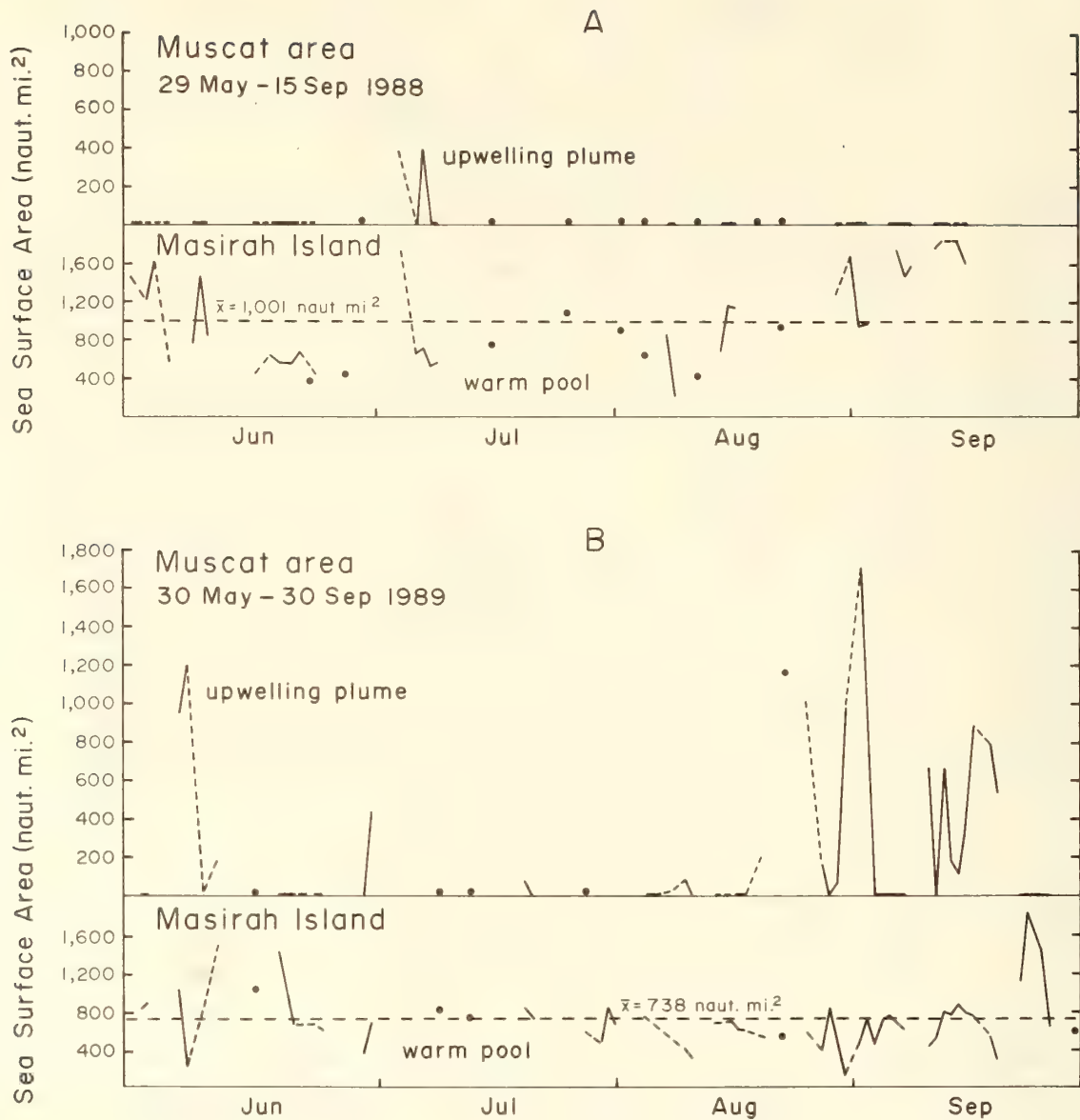


Figure 30. Upwelling activity in the Muscat area and persistence of a coastal warm pool along the lee side of Masirah Island during the monsoon season. The thermal changes are expressed in terms of sea surface area per 1° geographic quadrant for 1988 (A) and 1989 (B). Both plots in 1988 are based on 47 days each, and in 1989 on 58 days (Muscat) and 61 days (Masirah).

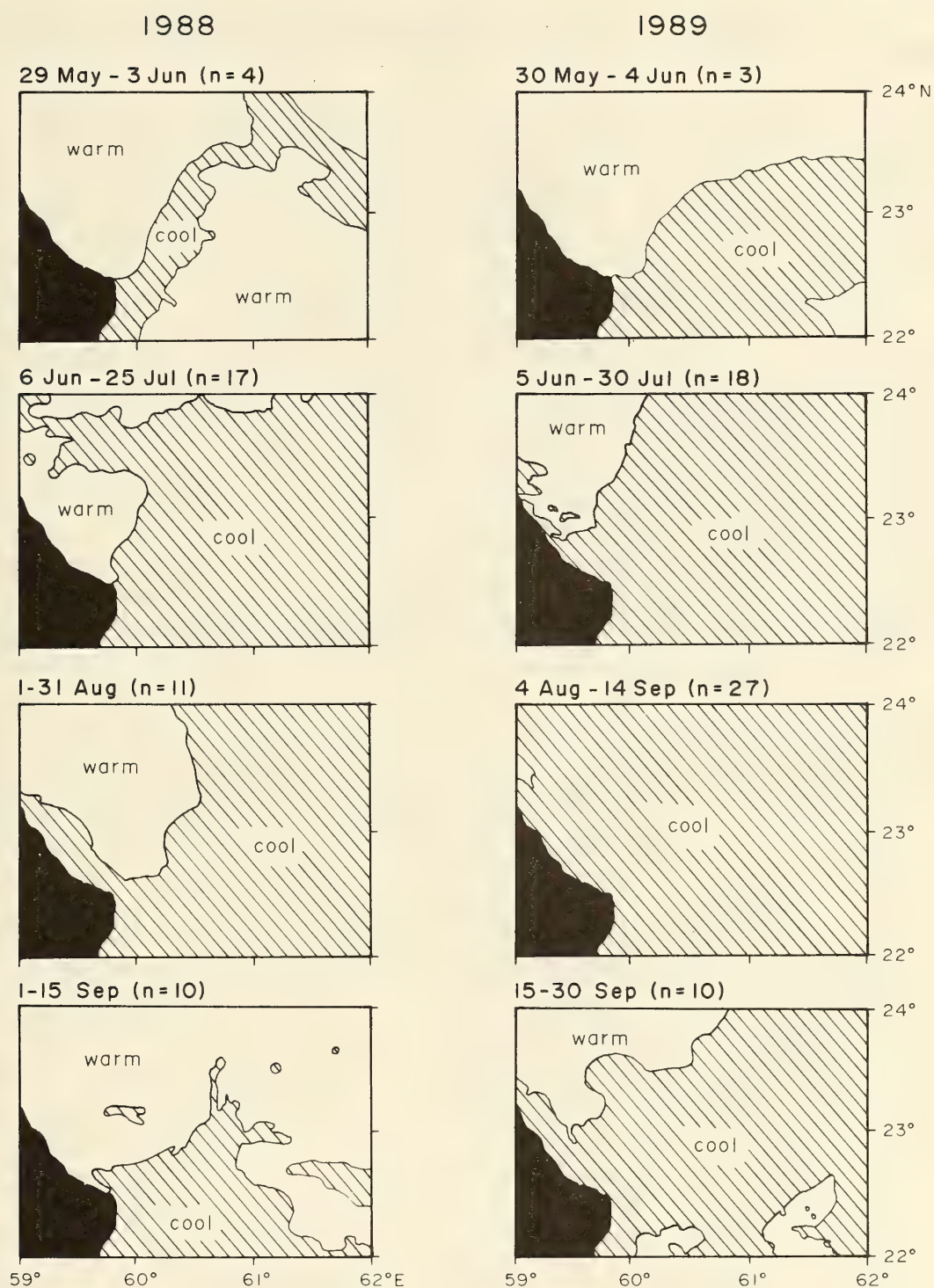


Figure 31. Development and spread of cold fronts near Ra's al Hadd during the summer monsoon periods in 1988 and 1989. Diagonal line patterns indicate the maximum penetration of cool Arabian Sea waters into the southern Gulf of Oman. Constructed from satellite SST images with observation dates and number of days examined indicated in each panel.

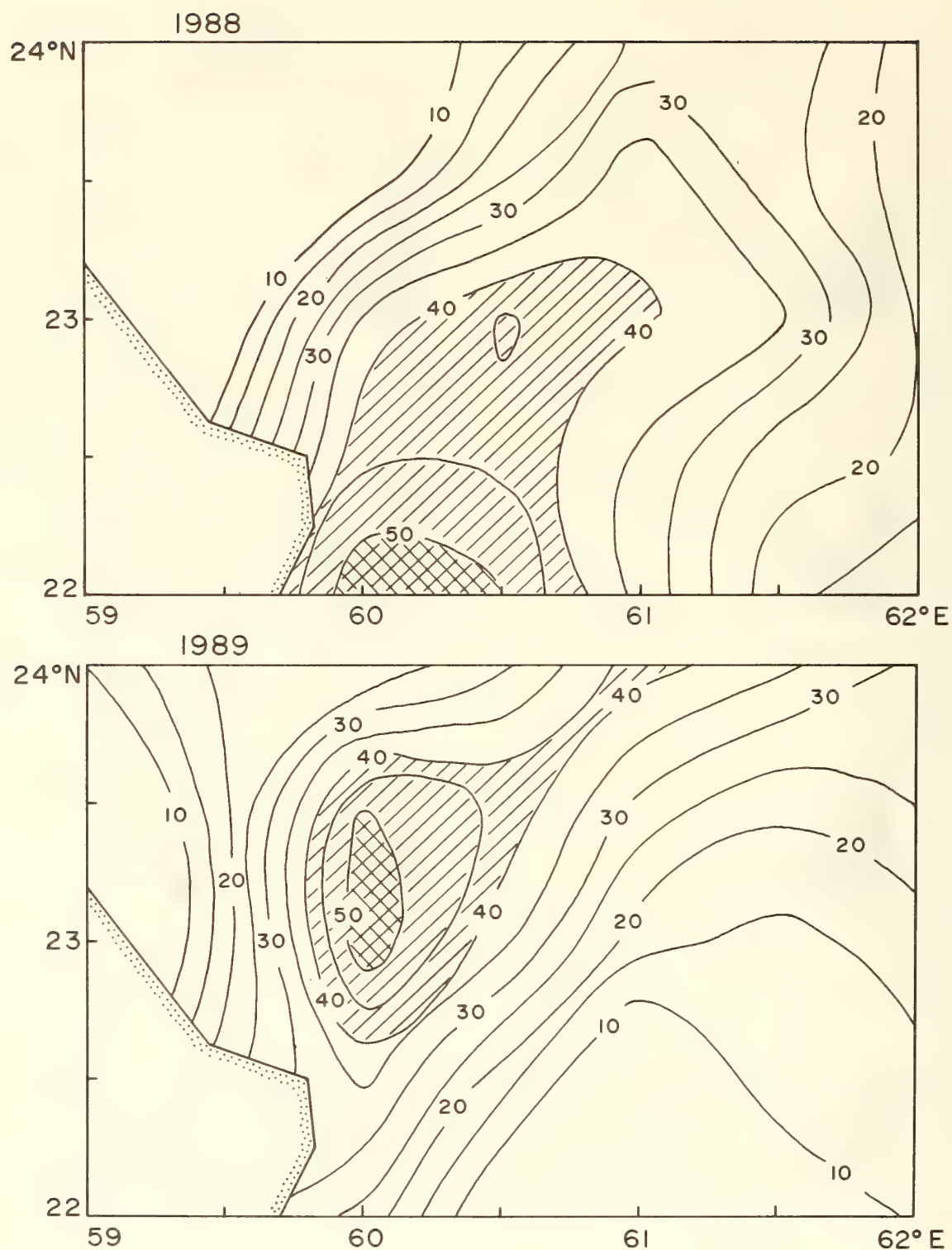


Figure 32. Percentage occupancy by area of the leading (northerly) SST cold fronts off Ra's al Hadd during the summer monsoon season in 1988 and 1989. Plotted in 0.5° quadrants from the minimum curve grid interpolation algorithm with a maximum absolute error of 0.005 and 500 iterations (Surfer, Golden Software, Inc.).

Status of the Crown-of-Thorns Starfish *Acanthaster planci*

Distribution and abundance. *Acanthaster planci* was observed only in the Gulf of Oman: at the Daymaniyat Islands, in the Capital area, at Ra's Abu Da'ud, and immediately west of Ra's al Hadd. *Acanthaster* occurred at 16 (41%) of the 39 sites surveyed in the Gulf of Oman. *Acanthaster* was present at 6 of 15 sites surveyed in the Daymaniyat Islands and demonstrated a median abundance of 60 ind/ha where present (Table 2). Population densities were high (70-140 ind/ha) at three sites (62, 70, 71). On the mainland coast, *Acanthaster* was present at 11 of 23 surveyed sites with a median density of 31 ind/ha (Table 3). The densest aggregation on the mainland, 63 and 84 ind/ha, occurred east of Sur (site 29) and at Bandar Jissah (site 17) respectively. A statistical comparison of the population densities in the Daymaniyat Islands with the mainland coast, at sites where *Acanthaster* was present, indicates that densities in the islands were significantly higher than on the mainland ($p = 0.05$, Mann-Whitney U test, 1-tailed test). However, when all sites are compared, including the 0 abundance observations (9 sites in the Daymaniyat Islands and 13 sites on the mainland), no significant ($p > 0.05$) difference was apparent.

Table 2. Abundance of *Acanthaster planci* in the Daymaniyat Islands (19 and 20 October 1982).

Locality	Site Number	Number <i>Acanthaster</i> Observed	Population Density (ind/ha)
W-most coral shoal	57	4	13
Jun (W-most island)	58	4	50
Small island E of Jun	59	16	49
Main group	62	7	70
Main group	70	14	140
Main group	71	3	100
Median =			60

Table 3. Abundance of *Acanthaster planci* along the mainland coast in the Capital and Sur areas (20 September - 24 October 1982).

Locality	Site Number	Number <i>Acanthaster</i> Observed	Population Density (ind/ha)
Jazirat Muscat	22	3	30
Pillar rock (yacht club)	75	1	20
Qantab	14	16	32
Bandar Jissah	17	42	84
Bandar Khayran	15	7	35
	23	12	17
Bandar Khayran (south)	56	25	31
Ra's Abu Da'ud	73	6	20
		14	18
Sur (ca. 20 km east)	29	11	63
Khor al Hair	28	5	36
Median =			31

Size measurements. *Acanthaster* disc diameters (cm) were measured at the following five localities with sample sizes indicated: Muscat, site 22 (n = 3 ind); Bandar Jissah, site 17 (n = 12); Bandar Khayran, sites 15 and 23 (n = 23); Ra's Abu Da'ud, site 73 (n = 20); Daymaniyat Islands, sites 57, 58, 62 and 71 (n = 16). Total diameter (TD) can be estimated from disc diameter (DD) according to the relation, $TD = DD/0.56$ (Glynn, 1982).

Statistical testing indicated a significant difference in *Acanthaster* sizes among the five localities ($p < 0.001$, Kruskal Wallis test). *A posteriori* testing (multiple comparisons procedure, $\alpha = 0.15$) indicated that starfish were significantly smaller at Muscat, Ra's Abu Da'ud and in the Daymaniyat Islands (Md DD = 16.0 cm) than at Bandar Jissah and Bandar Khayran (Md DD = 20.5 cm) (Figure 33).

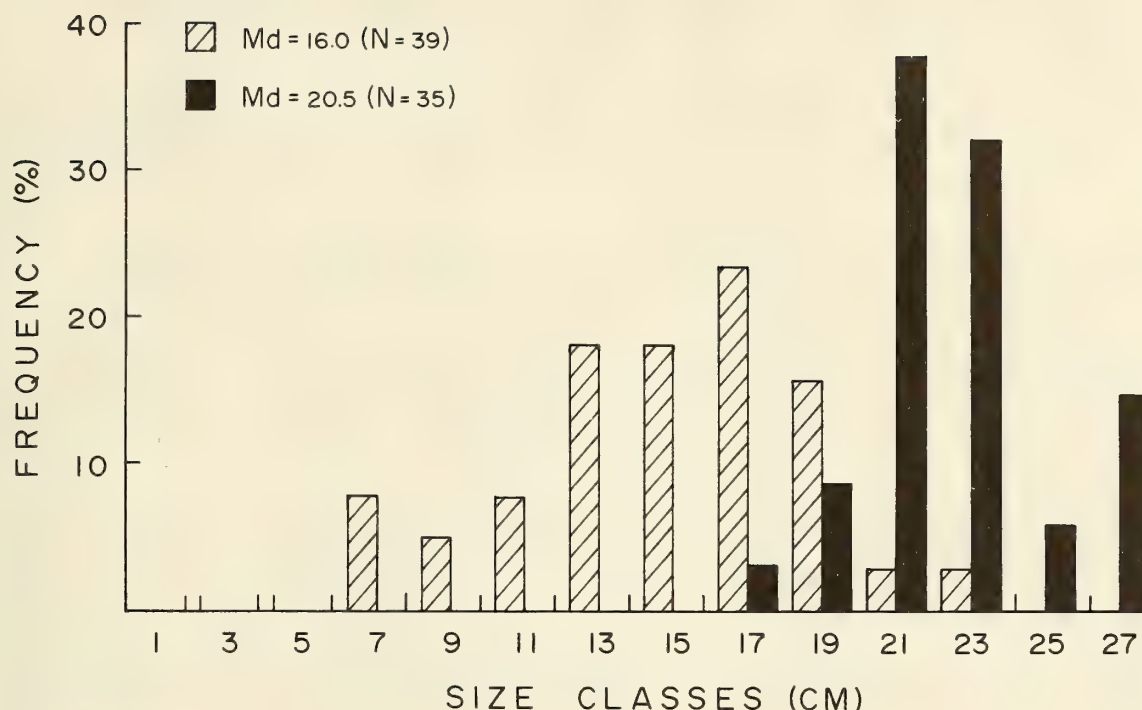


Figure 33. Size-class frequency distributions of *Acanthaster* sampled at Muscat, Ra's Abu Da'ud and the Daymaniyat Islands (cross-hatched bars), and Bandar Jissah and Bandar Khayran (solid bars). Combined median (Md) disc diameter and sample size (N) are noted for each distribution.

Search for juveniles. An effort was made to search for coral-feeding juvenile *Acanthaster* that could mature and impact coral communities later. Other than the 7-11 cm (12-20 cm TD) juvenile starfish found in the general censuses (Figure 33), no juveniles were seen in the various microhabitats searched in 8 areas, which involved a total effort of 8.7 man-hrs (Table 4). Small feeding scars occurred on corals in 3 areas (Sur, at a bay south of Bandar Khayran and in the Daymaniyat Islands), and it was assumed that *Acanthaster* caused these scars because they were observed near feeding starfish and other potential predators (e.g. gastropod corallivores) were not found.

Feeding observations. A quantitative assessment of the coral species attacked in the Daymaniyat Islands (site 62) revealed significant preferences for *Montipora* and *Acropora*, and an avoidance of *Pocillopora damicornis* (see Glynn, 1987). In the western Daymaniyat Islands (sites 57 and 58),

Table 4. Summary of search effort information for juvenile coral-eating *Acanthaster* (20 September - 20 October 1982). No *Acanthaster* juveniles were found during surveys.

Area	Sites	Microhabitats searched	Search time (man-hrs)
Musandam	4, 7	Basal branches of live and dead <i>Acropora</i> ; undersides of dead <i>Acropora</i> slabs.	50 min
Bandar Khayran	15, 17	Basal branches of live and dead <i>Acropora</i> and <i>Pocillopora</i> ; coral rubble bottom.	90 min
Suwadi	24	On live and dead ramose and massive <i>Porites</i> ; basal branches of <i>Pocillopora</i> and in pocilloporid rubble.	40 min
Sur	28, 29	Among and under massive <i>Porites</i> colonies with small feeding scars ¹⁾ ; under coral rock.	25 min
Marbat	32, 33	Basal branches of live and dead <i>Acropora</i> ; among rocks and under boulders.	120 min
Masirah	44, 45 49, 55	Among basal branches of live <i>Montipora</i> and <i>Pocillopora</i> ; under <i>Platygyra</i> colonies; under coral slabs.	55 min
Bandar Khayran (ca. 3 km south)	56	Among massive <i>Porites</i> colonies with small feeding scars ¹⁾ ; among live and dead <i>Acropora</i> and <i>Montipora</i> corals.	30 min
Daymaniyat Islands	57, 58 60, 70	Basal branches of <i>Acropora</i> with small feeding scars ¹⁾ ; under <i>Acropora</i> rubble; on live <i>Porites</i> and among basal branches of live <i>Pocillopora</i> .	110 min
TOTAL EFFORT:			8 hrs 40 min
TOTAL NUMBER JUVENILES FOUND:			0

1) *Acanthaster* were feeding in the vicinity and the freshly dead coral was presumed killed by adult or juvenile sea stars.

Acanthaster was observed feeding on *Pocillopora*, *Porites* and *Goniopora* with a significant preference for the latter genus. No live *Acropora* or *Montipora* were seen in the areas where *Acanthaster* was foraging. The only evidence of *Acanthaster* predation on all pocilloporid patch reefs was an occasional, freshly killed small colony or broken fragment of *P. damicornis* near the reef base.

Feeding scars typical of *Acanthaster* were seen occasionally on the mainland (sites 13, 21 and 74). Mostly small and broken fragments of *P. damicornis* had been eaten, presumably by *Acanthaster*, along the reef bases of pocilloporid reefs at sites 13, 21 and 22. *Acropora cytherea* was abundant at site 74 and this was the only species, of many present, that had been attacked. *Acanthaster* attacks on *Acropora* and *Montipora* were common where live colonies of these genera were abundant (e.g. sites 14, 15, 17, 23, 56 and 73). At most of these sites, numerous colonies appeared to have been killed recently by *Acanthaster*. Quantitative sampling indicated that *Acanthaster* preyed preferentially on *Acropora* at Bandar Khayran (site 15) and on *Montipora* at Ra's al Khayran (site 56) and Ra's Abu Da'ud (site 73). *Acanthaster* was observed feeding on massive *Porites* colonies at Khor al Hair (site 28). The small reef there consisted predominantly of *Porites* and *Goniopora* corals. Some coral taxa were seldom, if ever, observed being preyed upon by *Acanthaster* (e.g., *Astreopora myriophthalma*, *Echinopora* spp., *Platygyra* spp., *Acanthastrea echinata*, *Symphyllia radians* and *Turbinaria* spp.) even when present beside corals that were being eaten. All *Acanthaster* that were feeding at site 29 ($n = 10$ ind) were eating alcyonaceans. Reef corals were uncommon to rare at this site.

DISCUSSION

Pocilloporid Reefs and Inter-regional Comparisons

All pocilloporid coral communities and coral reef frameworks observed in this study occurred in habitats sheltered from strong wave action. On some reefs with large holes and separated pocilloporid blocks, visual inspection revealed that the reef framework accreted vertically as a meshwork of interlocking *Pocillopora damicornis* branches. These frameworks were highly porous, contained few binding coralline algae, and revealed no obvious post-depositional cementation. They are very similar to eastern Pacific pocilloporid reef structures (Glynn et al., 1972; Porter, 1972b; Glynn and Macintyre, 1977; Glynn and Wellington, 1983). Both Omani and

eastern Pacific pocilloporid reefs are fragile and typically develop under relatively calm-water conditions.

The *Pocillopora* assemblages described by Rosen (1971) at Mahe, Seychelles Islands, develop under markedly different conditions than those noted above. The Mahe pocilloporid assemblages were composed predominantly of colonies with an encrusting or robust growth form, which were tentatively identified as *Pocillopora danae-meandrina*. Moreover, the colonies were characteristically discrete, i.e. not forming contiguous patches, and generally increased in abundance under turbulent conditions such as shallow forereef habitats. These corals are closely allied, if not identical, to *Pocillopora verrucosa*, which is a well known Indo-Pacific species that typically inhabits exposed, reef front habitats (Veron and Pichon, 1976).

Although *P. verrucosa*/*P. meandrina* and *P. damicornis* communities develop under different conditions of water motion, they demonstrate similar cover/diversity relationships. Coral communities present in exposed habitats, e.g. at Mahe (Rosen, 1971) and also in Hawaii (Grigg and Maragos, 1974), tend to show decreasing coral species diversity as *Pocillopora* live cover increases. Grigg and Maragos (1974) suggested that increases in coral diversity were due to physical disturbances, which prevented the monopolization of space by competitively competent *Pocillopora* corals. This pattern also was observed in sheltered *P. damicornis* communities in Oman (present study) and the eastern Pacific (Glynn, 1976) with highest diversity on reef flats or in reef base zones. In Panamá, physical factors (e.g. extreme tidal exposures) were identified as diversifying agents at shallow depth and biological processes (e.g. predation, bioturbation) in deeper reef zones (Glynn, 1976).

Reef frames constructed by *P. damicornis* also occur at other outposts of reef development, i.e. in the western Arabian Gulf (Burchard, 1979), at several locations in the eastern Pacific region (Glynn and Wellington, 1983), and in western Australia (Veron and Marsh, 1988; Hatcher, 1991). Pocilloporid reef patches, occupying 100s of m² of bottom, were observed by Burchard (1979) in the western Arabian Gulf. The virtually monospecific stands of *Pocillopora* in the Arabian Gulf, which Burchard (1979) suggested might be of clonal origin, were present on current-swept reef knolls. Burchard (1979) did not comment on how clonal propagation might have occurred, but it is possible that water movement played some role. In the eastern Pacific, fragmentation of *Pocillopora* is caused by pufferfish that feed on colony branch-tips, incidental breakage by other foraging and nest-building fishes, bioerosion and wave action (Glynn et al., 1972; Wellington, 1982; Guzmán and Cortés, 1989). Since pocilloporid recruitment by sexually produced planula larvae is not frequent (Richmond, 1985; Glynn

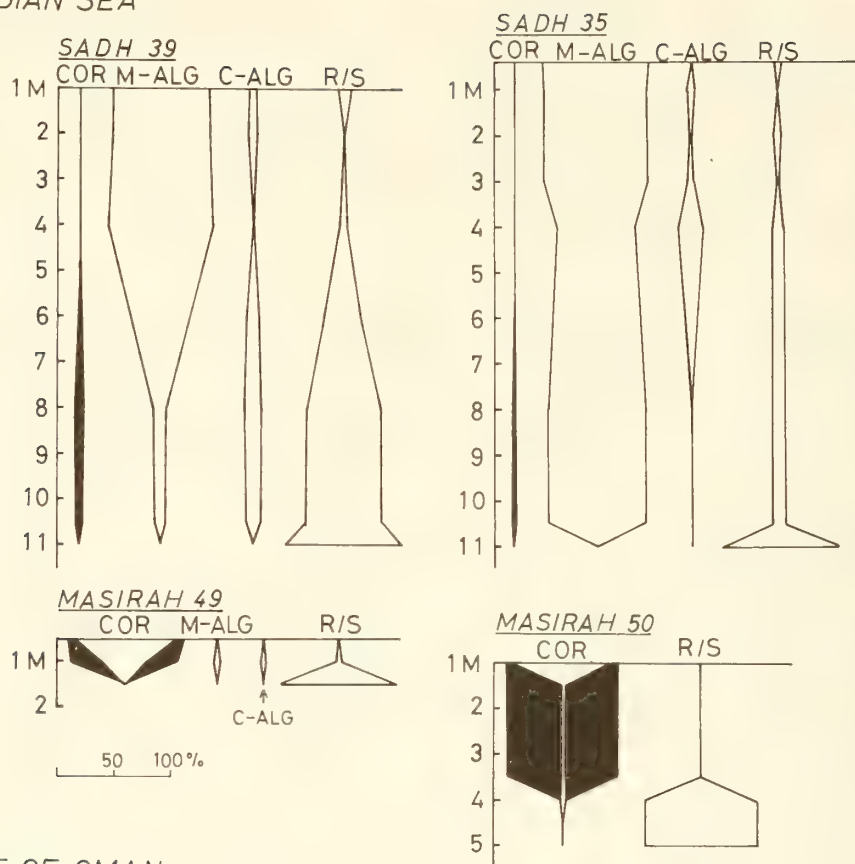
et al. 1991), the lateral spread of eastern Pacific *Pocillopora* reefs appears to be due mainly to asexual fragmentation (Highsmith, 1982). Stoddart (1983) found that asexual planula production was frequent in *P. damicornis* in western Australia (Rottnest Island). On the basis of a population genetic analysis and the growth morphology of post-juvenile colonies, he concluded that recruitment by asexual planulae was more important than fragmentation in reef growth.

The processes promoting the lateral growth of Omani pocilloporid reefs are not obvious. *P. damicornis* recruits were uncommon and relatively few *Pocillopora* fragments (dead or alive) were present. The general absence of large foraging fishes (herbivores and carnivores) or nest-building species, such as balistids and wrasses that often break and move corals in their building activities, suggests that this kind of disturbance may not be as important in Oman as it is in the eastern Pacific. Even on some pocilloporid reefs in the Daymaniyat Islands, where resident balistids (*Melichthys indicus*) were numerous, few broken coral branches were evident. In Hawaii, *Melichthys niger* (Bloch) feeds mostly on plankton, but occasionally eats coral (Hobson, 1974). Most reef base zones graded abruptly into sediment plains in Oman compared with extensive pocilloporid rubble slopes on eastern Pacific reefs. Possibly tropical cyclones play a role in coral fragmentation and horizontal reef growth (see below), however, the reefs that showed evidence of breakage in the Capital area were virtually devoid of live coral that would contribute toward reef recovery.

Upwelling Effects on Coral Reef Development and Distribution

This study revealed that coral communities and coral reefs were best developed in Arabian Gulf (Musandam) and Gulf of Oman (Daymaniyat Islands and Capital area) waters compared with the Arabian Sea coast of Oman, in general agreement with the findings of Green and Keech (1986), Sheppard (1988), Sheppard and Salm (1988), Sheppard et al. (1992) and Salm (1993). Coral cover and reef development were limited along the Arabian Sea coast except in a few areas sheltered from monsoon-induced upwelling. This difference is evident in the percent cover of coral and algal epibenthos in two areas (4 sites) on the Arabian Sea coast and one area (2 sites) in the Gulf of Oman (Figure 34). Macroalgae predominated at Sadh with only a few reef-building corals present below about 5 m. The most notable difference between Masirah and Muscat was the shallow occurrence of corals in the Arabian Sea area (to 4 m depth) compared with the Gulf of Oman (to 11 m depth). These results also agree with other studies that have

ARABIAN SEA



GULF OF OMAN

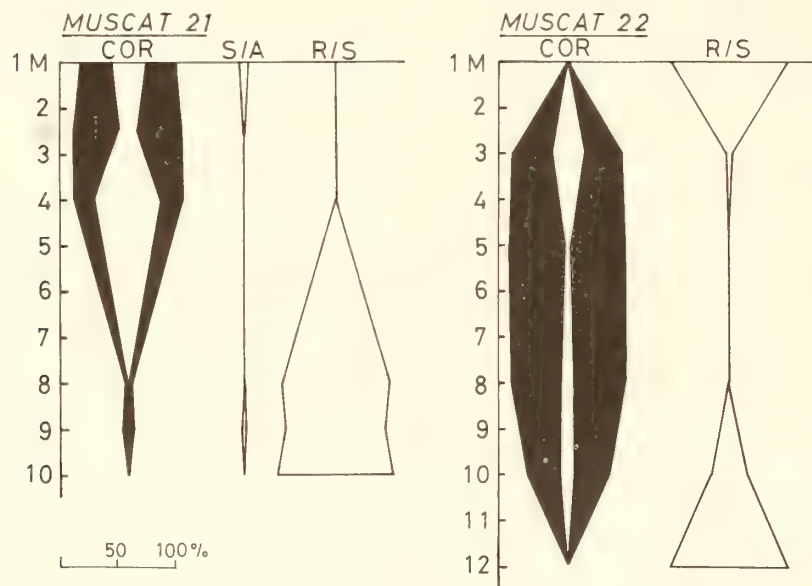


Figure 34. Percent cover with depth of major epibenthos at four sites in the Arabian Sea and two sites in the Gulf of Oman. COR, reef-building corals (solid = live, open = dead); M-ALG, macroalgae; C-ALG, coralline algae; R/S, rock and/or sand; S/A, sponges and/or sea anemones.

demonstrated a negative influence of upwelling on reef growth in the Indian Ocean (Scheer 1971, 1984; UNEP/IUCN, 1988) and elsewhere (Ladd, 1971; Glynn and Stewart, 1973; Sournia, 1976; Antonius, 1980; Glynn and Wellington, 1983).

Two areas in the Arabian Sea not investigated in this study, Barr al Hikman and the Kuria Muria Islands (Al Halaniyat), have been shown to support extensive reef development, and diverse and abundant coral communities (Salm, 1993). Most of the coral reefs off Barr al Hikman, Gulf of Masirah, are built chiefly of *Montipora foliosa*, occupy many square kilometers, and are the largest reef structures in the Sultanate (Salm, 1993). The distribution of the Barr al Hikman reef complex corresponds with the typically warm thermal conditions observed in the northern sector of the Gulf of Masirah.

In some bays on the mainland Dhofar coast and in the Kuria Muria Islands, maximum live coral cover was 99%, *Porites* colonies attained 12 m in diameter, and several reef associated cnidarians (e.g., *Tubipora*, *Millepora*, *Gardineroseris*, *Goniastrea*, *Euphyllia* and *Leptoria*) were found that are not known from other parts of the Sultanate (Salm, 1993). True reef development, with *Porites* constructing up to 3-m thick frameworks, also were observed at 17 sites in the Dhofar Province. Sheppard et al. (1992) noted the occurrence of coral reefs at Ra's Madrasah (Figure 27), but offer no information on location, size or species composition. The 8 sites I examined on the Dhofar coast revealed scant coral cover ($\leq 10\%$), no reef frameworks, and no new coral genera. The bottom cover at all sites consisted of 80-90% macroalgae. The diverse and well developed coral formations reported by Salm (1993) were unexpected because of the active upwelling that occurs along the Dhofar coast. According to Savidge et al. (1990), the main upwelling area off the southern coast of Oman is likely localized in the immediate vicinity of the Kuria Muria Island chain. During the 1984 SW monsoon season, minimum SSTs of 16.2°C were recorded from a site approximately 1 km offshore in Kuria Muria Bay (Savidge et al., 1990). Several workers have reported the coldest upwelled water to occur on the downstream (eastern) side of headlands, off Ra's Hasik (approximately 40 km W of the Kuria Muria Islands), off Ra's Suqrah, and Ra's Madrasah, in the southern sector of the Gulf of Masirah (Currie et al., 1973; Weeks, 1983; Elliott and Savidge, 1990; Savidge et al., 1990; Brock et al., 1992; present study).

Exceptionally large coral colonies are known from upwelling regions, e.g. the 12 m diameter colony of *Pavona* in Urvina Bay, Galápagos Islands (Colgan, 1990). However, this colony was located on the lee side of Fernandina Island, which sheltered it from the most intense upwelling of the

region (Colgan, 1991). In addition, the best developed coral formations in the Galápagos Islands and Pearl Islands (Panamá) are located on island shores that are not exposed to the most intense upwelling in these regions (Glynn and Stewart, 1973; Glynn and Wellington, 1983). Also, the occurrence of several tropical coral genera only in the upwelling Dhofar area (Salm, 1993) is inconsistent with known distributional patterns in upwelling eastern Pacific environments. For example, 3 species of *Millepora* are known from the non-upwelling Gulf of Chiriqui, Panamá, while none has been reported in the upwelling Gulf of Panamá (Glynn et al., 1972; Porter, 1972b). Clearly, detailed studies are now in order to determine fine-scale upwelling patterns and how these relate to coral community distribution and development in the Dhofar.

The occurrence of several tropical species of corals, echinoderms and fishes in the Dhofar and not elsewhere in Oman is intriguing. Salm (1993) briefly noted that some of the extant Dhofar coral species may represent Pleistocene relicts since they are also found as fossils in beach gravel deposits along the Gulf of Oman coast from Ra's al Hadd to Sur. It is also possible that such species represent ephemeral Holocene populations that experience relatively brief periods of invasion and extinction. Monsoon-driven currents could convey propagules from the east African coast during the SW monsoon and from northeastern Arabian Sea localities (e.g., Pakistan and India) during the NE monsoon (Bauer et al., 1991). Considering the strong upwelling conditions that accompany the SW monsoon, I believe that non-upwelling NE monsoon currents would offer a more suitable means for the conveyance of tropical larvae along the southern coast of Oman. Other examples of current systems that likely advect larvae into marginal reef environments from tropical source areas are the Leeuwin Current off western Australia (Hatcher, 1991), the Kuroshio Current off southern Japan (Tribble and Randall, 1986; Yamaguchi, 1986; Veron, 1992), and the North Equatorial Counter Current that flows into the eastern Pacific (Dana, 1975; Richmond, 1990; Glynn and Colgan, 1992).

Nutrient pulses that accompany upwelling promote the growth of benthic algae, which may interfere with coral growth and survivorship through increased competition (Glynn and Stewart, 1973). A similar argument has been advanced to explain the latitudinal limits of coral reef growth, which seem to be influenced by low water temperature, high nutrient levels and abundant macroalgal populations (Johannes et al., 1983; Hatcher, 1985, 1991). Dissolved nutrient concentrations increase dramatically along the Dhofar coast during the SW monsoon period. For example, $\text{NO}^3\text{-N}$ demonstrated a 10-fold increase during upwelling, from 2-3 to 20-22 $\mu\text{g-at.l}^{-1}$, and $\text{PO}^4\text{-P}$ a 2-3 fold increase, from 0.75-0.80 to 1.9-2.0 $\mu\text{g-at.l}^{-1}$ (Savidge et al., 1990). The elevation in nutrient levels shows a high seasonal correlation

with increases in benthic algal biomass (Barratt in IUCN/ROPME/UNEP, 1985; Sheppard et al., 1992). Unlike upwelling-dependent, macroalgal ecosystems elsewhere, the Dhofar kelp forests undergo a marked seasonal die-back. Barratt noted a "...total annual decline and recovery with the life cycles of the relevant species being completed in a time span of only six months." Thus, reef corals on the Arabian Sea coast of Oman can tolerate the seasonal proliferation of macroalgae as do corals in the Arabian Gulf (Coles, 1988).

Upwelling also occurs in the Gulf of Oman during the summer (June-September) monsoon season, but is more localized and sporadic compared with upwelling on the Arabian Sea coast. Green and Keech (1986) noted the high interannual variability of upwelling in the Capital area. This variability was evident in the present study as well: a single, spatially restricted upwelling pulse was observed in the Capital area in 1988 whereas several, widespread upwelling plumes occurred in 1989. Green and Keech (1986) reported a 15°C temperature drop (from 32° to 17°C) observed at 10 m depth in just under two weeks during an upwelling event in July 1983. It was speculated that such sudden temperature drops might be responsible for areas of dead coral observed on reefs in upwelling environments. The youthfulness of coral formations and the absence of certain coral genera in the Capital area also were attributed to upwelling disturbances (Green, 1983). In light of the many distinctive coral genera that are restricted to strong upwelling conditions along the Arabian Sea coast (Salm, 1993), the latter suggestion is not very convincing.

Acanthaster: Distribution, Abundance and Effects on Coral Communities

Surveys conducted through 1990, spanning a 7 year period since this 1982 study, have confirmed that *Acanthaster* is limited in distribution to the Gulf of Oman (Salm, 1993). *Acanthaster* was not found at any of the Musandam sites in the 1982 study. However, on the north coast of Musandam (Kumzar, site 10), the easternmost site surveyed in 1982, large adults of *Acanthaster* were locally abundant in 1989-90. No *Acanthaster* were found on the west or Arabian Gulf side of the Musandam in later surveys, but outbreak populations were seen at several sites along the north and east shores or Gulf of Oman side of the Musandam. Environmental conditions (i.e. warm thermal regime, abundant coral prey) appeared to be favorable for *Acanthaster* on the Arabian Gulf side, and its apparent absence there was unexpected. Salm (1993) has suggested that current eddies characteristic of areas of complex coastal terrain could be responsible for concentrating coral and *Acanthaster* larvae at Musandam sites bordering the Gulf of Oman. Modelling results of the larval dispersal of *Acanthaster* on the

Great Barrier Reef have demonstrated a focusing of recruitment from multiple sources by currents (Dight et al., 1990).

Acanthaster was not seen in two areas (Masirah and Dhofar) on the Arabian Sea coast in 1982 nor in later surveys, including the Kuria Muria Islands (Salm, 1993). Several factors could be responsible for the absence of the starfish from this region. Regarding the relatively high thermal conditions necessary for *Acanthaster* to reproduce and complete larval development (25°-32°C; Lucas, 1973; Moran, 1986) -- spawning typically occurs between May and August in the northern hemisphere when sea temperatures are high -- it is clear that the Arabian Sea coast of Oman would not offer suitable conditions during most of the summer (June-September) when the monsoon jet from northeastern Africa induces active upwelling (16°-19°C). If it were possible for *Acanthaster* to reproduce in the early summer (May and June), then it is likely that later developmental stages could be adversely affected by at least two factors. The high population abundances of suspension feeders inhabiting this upwelling environment would pose a risk to the larvae, and coral prey required by the young adults would generally be in low supply and highly dispersed. Still, high coral abundance and moderate thermal environments do occur along the Arabian Sea coast, e.g. in the northern Gulf of Masirah, indicating the presence of suitable conditions on local scales. A similar situation occurs off the eastern tropical Pacific coast where the southern limit of distribution of *Acanthaster* corresponds with a marked thermal front that separates non-upwelling and upwelling waters (Glynn, 1974). Certain areas to the south support vigorous coral reef development, e.g. Gorgona Island, Colombia (Glynn et al., 1982), yet *Acanthaster* has not been reported from these localities.

Although the MAF had received several reports of *Acanthaster* outbreaks in the Daymaniyat Islands and Capital area, these were largely unsubstantiated. Commercial fishermen and sports divers claimed that several hundreds of *Acanthaster* per hectare were feeding on reef corals at several sites in the Gulf of Oman. The only quantitative data that I could find reported two *Acanthaster* in a 100 m transect at Fahal Island (near site 13, Figure 4), and 0.5 ind/m² (25 ind/50 m²) at Bandar Jissah (Interim Report, 1982; Glynn, 1983a). If the latter density could be extrapolated realistically to a larger area, then this would be equivalent to an outbreak population (100s of ind/ha; Moran, 1986).

The population densities reported in this study and the earlier survey at Bandar Jissah probably are oppositely biased by two effects: 1) the counts were made in restricted areas and represent starfish that had aggregated while feeding, and 2) the searches were conducted during daylight hours when some resting starfish were hidden from view. Fresh feeding scars

attributed to *Acanthaster* were noted at three sites where no starfish were observed. I believe that these field procedures tend to inflate starfish abundances. If surrounding areas of coral habitat, with few or no starfish present, were added to the sampled areas then the starfish densities in many cases would surely be lower than reported.

After 1982, the highest abundances of *Acanthaster* were reported from the Gulf of Oman shores of the Musandam (Salm, 1993). In the Habalayn area (about 10 km SE of Khasab), 27 *Acanthaster*/0.4 ha were observed in 1986, and 117 ind/15 min (the largest number seen) were reported during the 1989-90 survey. Although highly variable abundances have been observed at various Indo-Pacific localities (Moran, 1986), the former density (68 ind/ha) is higher than any reported normal population, and the latter corresponds with most outbreaking populations. *Acanthaster* has remained relatively common in the Muscat area during the past decade (Salm, 1993).

On the basis of field studies in the western Pacific (Kenchington, 1977; Zann et al., 1987), *Acanthaster* can attain disc diameters of 14-20 cm in a period of 3-4 years. Therefore, it is probable that most individuals observed in late 1982 originated locally from the abundant populations reported during 1978-1980. The considerable range in starfish sizes may result from two effects: (1) populations composed of smaller individuals are relatively youthful; (2) the size differences reflect the abundance of coral food resources (Dana et al., 1972). In support of the food-abundance explanation, the largest starfish were present in areas with the highest abundance of *Acropora* corals, i.e. at Bandar Jissah and Bandar Khayran.

Much effort was spent in the 1982 survey searching for juvenile starfish that could mature and affect coral communities at a later time. Since very few juveniles (7-9 cm disc diameter) were found in the Gulf of Oman surveys, no large-scale outbreaks were predicted through late 1984 (Glynn, 1983a). Evidently, all areas of the Gulf of Oman south of the Musandam have been free of *Acanthaster* outbreaks since the 1978-80 episode (Salm, 1993).

Acanthaster fed disproportionately on *Acropora* and *Montipora* species at all sites in the Gulf of Oman where these corals were abundant (Glynn, 1987). However, where *Acropora* and *Montipora* were uncommon or absent -- in several areas only dead colonies of these genera remained after presumed earlier starfish attacks -- *Acanthaster* fed on *Porites* spp., *Goniopora* spp., *Stylophora pistillata*, *Pocillopora damicornis*, and other corals. Several field studies have shown that *Acanthaster* feeds preferentially on acroporid corals (e.g. Branham et al., 1971; Glynn, 1983b, 1987; Moran, 1986; Colgan, 1987; Faure, 1989; Keesing, in press). Pocilloporids also have been named as

preferred prey in some studies (Porter, 1972; Ormond et al., 1976; Glynn, 1983; Faure, 1989; Keesing, in press). However, when the supposed preferred prey species is *P. damicornis*, this claim is usually based on qualitative evidence (Potts, 1982). That is, the number of consumed prey is not related to prey availability. Moreover, the spatial distribution of colonies, i.e. dispersed versus aggregated, is seldom mentioned. *P. damicornis* colonies within monospecific patches are seldom attacked by *Acanthaster* (Glynn, 1976). *Acanthaster* commonly feeds, however, on the broken branches of *P. damicornis*, which contain few if any crustacean guards, around the edges of pocilloporid patches.

Many *Stylophora* (Pocilloporidae) were eaten by *Acanthaster* in Oman despite the defensive maneuvers of their crustacean guards. *Acanthaster* also demonstrated a strong preference for both mature and juvenile *Stylophora* in American Samoa (Glynn, 1983b) and Okinawa (Keesing, in press) respectively. It is possible that the lower guard densities/colony and lower level alpheid guard defensive responses in *Stylophora*, compared with *Pocillopora* (Glynn, 1983b, 1987), is at least partly responsible for the different susceptibilities to predation in these genera. Another factor may relate to the spatial distribution of the prey taxa. That is, *Stylophora* colonies typically are dispersed whereas *P. damicornis* colonies frequently form thickets. Dispersed colonies could be more susceptible to predation than aggregated colonies.

Coral communities in many parts of the Gulf of Oman are recovering following high levels of *Acanthaster* predation and are in a nonequilibrium state (Connell, 1978). Where predation was severe coral cover and diversity demonstrated a notable decline. The recruitment of *Acropora* and *Pocillopora* has been observed in some affected areas (Salm, 1993), but the course of recovery cannot be predicted without knowledge of continuing *Acanthaster* predation and patterns of coral recruitment. In the western Pacific, rapid recovery (ca. 10 years) has occurred on some reefs that experienced intense and short-lived predation and high recruitment following *Acanthaster* outbreaks (Pearson, 1981; Colgan, 1987). However, if *Acanthaster* abundances remain relatively high in the Gulf of Oman, i.e. around 30 ind/ha, and coral recruitment is low, recovery of acroporid reefs could be prolonged (perhaps spanning decades).

This recovery scenario would be exacerbated if *Acanthaster* continues feeding selectively on remnant and recruiting acroporid corals (Keesing, in press) as occurred on an Okinawan reef subject to persistent *Acanthaster* predation since the early 1970s (Nishihira and Yamazato, 1974; Yamaguchi, 1986). Keesing (in press) found that medium population levels of *Acanthaster* (33-44 ind/ha) that continued feeding selectively on recruiting

acroporid and pocilloporid corals interfered with recovery, resulting in a community dominated by non-preferred *Porites*, *Millepora*, and alcyoniid soft corals. The destructive grazing effects of high sea urchin [*Echinometra mathaei* (de Blainville)] densities on the Okinawan reef also were suspected of interfering with coral recruitment. This effect on Omani reefs has not been investigated.

The results of the 1978-80 *Acanthaster* outbreak, particularly in the Daymaniyat Islands, had a devastating impact on acroporid reefs. Virtually all acroporid corals were killed. In mixed coral assemblages, where acroporid, montiporid, pocilloporid, and poritid corals occurred side by side, only acroporid/montiporid taxa were killed in large amounts. Several reefs composed mainly of *Porites* and *Pocillopora* corals were still largely intact, exhibiting 80-100% live cover. This scale of predation would seem to affect the differential survival of reef types. Perhaps the prominence of poritid and pocilloporid corals in the Gulf of Oman is in large degree mediated by *Acanthaster* predation, both at outbreak and long-term moderate levels. The prominence of acroporid and montiporid communities and reef frameworks on the Arabian Gulf side of Musandam, and at sites protected from intense upwelling on the Arabian Sea coast, also may be related to the absence of *Acanthaster* in these areas.

Other Factors Affecting Omani Coral Reefs

Unlike the large stands of dead *in situ* *Acropora* observed in the Daymaniyat Islands and Capital area, the dead *Pocillopora* reefs from Bandar Jissah south to Ra's Abu Da'ud, a coastal stretch of 37 km, showed clear signs of mechanical destruction. The summits of these reefs were planed level and large amounts of coral debris were found nearby. Considering the large scale of this damage and lack of fishery-related artifacts, other sorts of disturbances should be considered. Since the Gulf of Oman and Arabian Sea are located within a center of tropical cyclones (Stoddart, 1971a), it is possible that these fragile pocilloporid reefs were damaged by a severe storm. It is also possible that the dead, *in situ* pocilloporid reef framework observed at Masirah Island could have resulted from a storm similar to that which crossed Masirah on 13 July 1977 (Everts et al., 1983). This storm had maximum sustained winds of 46.3 m/sec, maximum wind gusts of 61.7 m/sec, and resulted in 430.6 mm of precipitation over a 24 hr period. Some potential impacts from a storm of this magnitude that could kill corals yet not affect their growth position are (1) sea water dilution resulting from heavy rainfall and river flooding, (2) drop in water level due to altered reef geomorphology, and (3) deposition of sediment on live corals (Stoddart, 1971b).

Widespread and locally severe coral reef bleaching (zooxanthellae and/or chlorophyll pigment loss) was reported for the first time in the Gulf of Oman during the summer of 1990 (Salm, 1993). Reef corals, alcyonaceans and zoanthids were affected in the Muscat area and on the eastern shores of the Musandam Peninsula. The bleaching event revealed the following responses, which have been related to elevated SSTs in other regions (Brown, 1990; Glynn, 1990b, 1991; Williams and Bunkley-Williams, 1990): 1) severity greatest during peak summer temperatures; 2) shallow reef populations most affected; 3) populations in areas with reduced circulation most affected; and 4) duration of exposure, with SSTs in excess of 30°C, was critical.

Although near-shore temperature data are not available to assess the intensity and duration of elevated SSTs in 1990, the Nansen cast record reported in this study suggests that the June 1990 SSTs were exceptionally warm. For example, the 39°C SST reported near Muscat (Salm, 1993) was 2°C higher than the maximum June temperature recorded during the 46 year period of record. The 35°C SSTs recorded in the Musandam in August 1990 also were 1°C above the long-term maximum temperature for this month in the Gulf of Oman. Additionally, remote sensing SST data from the Muscat area in the summers of 1988 and 1989 showed that near-shore high temperatures were in the range 31°-33°C, which agree with earlier (1965 and 1966) summer maximum temperatures of 30°-32°C recorded at 1.8 m depth at Mina al Fahal (Green and Keech, 1986). Satellite SST data from 1990 were not analyzed.

Bleaching-induced mortality in the Muscat area was slight (<2%) and affected only *Acropora*. *Montipora* and *Porites* were severely bleached, but recovered when SSTs normalized. Mortality was greater in the Musandam, but highly variable, ranging from <1% to >95%. Many of the affected coral species (*Acropora* and *Stylophora*) were species also selectively preyed on by *Acanthaster*. *Platygyra daedalea* experienced high partial mortality and dead patches were invaded by algae and presumably later heavily bioeroded by sea urchins. Salm (1993) speculated that the many hollowed-out, live *P. daedalea* in this area might result from sporadic bleaching events such as that observed in 1990. Interestingly, Salm (1993) did not report bleaching in *Pocillopora damicornis*, a highly susceptible species in other regions (Brown, 1990; Glynn, 1990b). The upper branches of numerous shallow (0.5-1 m depth) *P. damicornis* colonies were bleached on the Arabian Gulf side of Musandam (site 12) on 21 September 1982. This was the only coral bleaching observed at that time.

The differences in severity of bleaching and mortality in the Muscat and Musandam areas were hypothesized by Salm (1993) to be related to local differences in circulation processes. Although higher SSTs were recorded in

the Muscat area than at Musandam, temperatures dropped rapidly at Muscat, from 39°C to 24°C in less than one week at the end of June. This sudden temperature drop likely was due to upwelling. Upwelling has not been reported at Musandam, and there SSTs in 1990 remained above 30°C to a depth of 10 m for at least three months. In the Gulf of Panamá, upwelling moderated sea warming during the 1982-83 El Niño event, delaying coral bleaching and mortality by four months (Glynn, 1984).

Other factors impacting Omani coral reefs, such as coastal erosion, flooding, sedimentation, possible coral diseases, and several types of anthropogenic disturbances are enumerated by Salm (1993). Entangling fishing nets, anchor damage and other fishery-related impacts are prevalent in the Musandam and Capital areas. Fragile *Acropora* and *Pocillopora* assemblages in particular have been subject to widespread destruction during the past decade. Salm (1993) reported that litter and fishery activities have caused notable damage to coral communities at 72% of 111 sites surveyed in the Musandam, 61% of 43 sites in the Muscat area, and 35% of 20 sites in the Dhofar Province. I did not witness any obvious human-related damage to coral communities in 1982, during concentrated surveys at 75 sites distributed across the Sultanate. Besides the unfortunate degradation of numerous, formerly pristine, coral sites in recent years, in many damaged areas it will now be impossible to distinguish between natural and anthropogenic causes. This will greatly complicate management procedures because of the increasing difficulty in assessing the impact of human activities.

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NO. 380

CORAL REEFS OF THE SULTANATE OF OMAN

BY

RODNEY V. SALM

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CONTENTS

	Page
INTRODUCTION	1
Background	1
Objectives	2
Methods	2
 DISTRIBUTION AND NATURE OF CORAL COMMUNITIES	 5
Influences on Coral Occurrence and Growth	5
The Nature of Corals and Coral Communities	6
Coral Diversity	10
Coral Communities of Musandam	11
Coral Communities of the Muscat Area	14
Coral Communities of the Gulf of Masirah Area	15
Coral Communities of Dhofar	16
 THREATS TO CORAL COMMUNITIES	 18
Fishery Related Damage to Coral Communities	19
<i>Acanthaster planci</i>	20
 REFERENCES	 26
 APPENDIX 1. CORAL LISTS	 29
 APPENDIX 2. DESCRIPTIONS OF CORAL COMMUNITIES IN OMAN	 41
 APPENDIX 3. SUMMARY OF CORAL BLEACHING OBSERVATIONS, MUSANDAM	 82

LIST OF TABLES

Table 1. List of coral genera by region of Oman	12
Table 2. Corals eaten by <i>Acanthaster planci</i> in Oman	21
Coral Bleaching in the Sultanate of Oman	22

LIST OF FIGURES

Figure 1. Distribution of coral and coral study sites in Oman	4
Figure 2. Genus-discovery curves for corals on "monogeneric" reefs	8
Figure 3. Genus-discovery curves for corals in mixed assemblages	8
Figure 4. Genus-discovery curves for corals in the primary successional stages of reef development	9

CORAL REEFS OF THE SULTANATE OF OMAN

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RODNEY V. SALM

INTRODUCTION

Background

Corals and coral communities in Oman have been described for the Musandam area in the north (Glynn 1983), the Muscat Area (Green 1983, 1984; Green & Keech 1986; Glynn, 1983; Salm & Sheppard 1986), Masirah Island (Glynn 1983), Dhofar in the south (Barrat 1984, Glynn 1983), and for Oman generally (Sheppard & Salm 1988).

Coral diversity has been mapped for the Muscat Area (IUCN 1986) and, in more detail, for specific sites within it (Salm 1986a), for the southern Gulf of Oman (IUCN 1988), Dhofar (IUCN 1989b), and Musandam (IUCN 1991). Coral records of the IUCN Coastal Zone Management (CZM) Project were incorporated into a computerized database using DBase III Plus for 185 sites spanning the entire coast of the Sultanate (Appendix 1). The database also classifies these sites by the type of coral assemblage (i.e., coral reef with framework development or rock with non-reef coral community), and provides general descriptions of the site and information on the uses and threats to corals there.

This report is an interpretation of the database, and a second general environmental classification database that provides details of uses and management issues for 330 sites, of which 246 have coral communities (Appendix 2). It presents additional information on the corals of Oman, resulting from studies directed specifically toward the formulation of coastal zone management plans (CZMPs) and overview reports covering the entire coast of the Sultanate.

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Objectives

Coral communities were surveyed between November 1984 and June 1992. The aim of these surveys was to identify areas that were most valuable for conservation, and hence least suitable for major coastal works, such as marinas, fishing boat harbours, or effluent outfalls from desalination plants, sewage works or other sources.

The objectives of the surveys were to:

- 1) compile a comprehensive list of corals found at each study site;
- 2) map the distribution of coral communities;
- 3) select candidate sites for conservation of coral communities based on coral diversity (measured as richness of coral genera and species), percentage cover of corals, degree of reef framework development, presence of unusual corals or coral formations, and/or representativeness of coral assemblages for each section of coast;
- 4) identify uses of coral environments and their impacts, and other natural or people-related threats;
- 5) define management issues, and specify actions and responsibilities to resolve these; and
- 6) compile named collections of corals for presentation to the Oman Natural History Museum.

Methods

The study area includes the entire coast of Oman, extending from the Arabian Gulf coast in the north to the Yemen border in the south, and including all offshore islands.

The likely location of coral communities was determined from aerial photographs, helicopter overflights of most of the study area, and boat and underwater reconnaissance.

Corals were identified and recorded *in situ*, while snorkeling or scuba diving, at a total of 170 specific sites (Figure 1). Regional coral records were supplemented by beach specimens or underwater sightings made in addition to the detailed listings. Representative collections of corals from each region (Musandam, Muscat area, Masirah area, Dhofar) were made for reference. Corals that could not be identified underwater were collected, cleaned, and identified by comparison with the reference collections, or from the following texts: Burchard (1980), Scheer & Pillai (1983), Veron & Pichon (1976, 1980, 1982), Veron & Wallace (1984), Veron, Pichon & Wijsman-Best (1977), Wells (1956). All coral specimens were presented to the Oman Natural History Museum (contact: Curator, Oman Natural History Museum, Ministry of National Heritage and Culture, P.O. Box 668, Muscat, Sultanate of Oman).

Corals were recorded by the following standard procedure developed to enable rapid comparative surveys of numerous reef areas.

Upon entry into the sea, several minutes were devoted to orientation and recording the nature of substrate and coral community (percent cover, angle of slope, presence of reef framework, dominant and predominant corals). Next, corals were recorded continuously in sequential five minute intervals onto a plastic slate for generally 30 minutes. This procedure yielded a characteristic genus-discovery curve (total genera x five minute interval) for each study site (Figures 2, 3, 4).

This genus-discovery method, described in more detail below, was developed by me to enable rapid survey of reefs and facilitate comparative assessment of coral diversity over vast tracts of the Indonesian Archipelago. The principle is one of non-random focussed search for different coral genera over a 30 minute period. The search covers as many different zones and habitats as possible (typically in this order: reef crest, slope, edge, gullies, walls, overhangs, caves, reef-flat) to yield the greatest possible variety of corals during the time period. Corals are identified to genus *in situ*, and recorded onto a plastic slate. Each 5-minute interval is marked. This yields a total genus count per 30 minutes for each coral community (the richness index), and a count of additional genera per 5-minute interval. The yield of additional genera drops with each successive 5-minute interval.

The total number of genera plotted over the six successive 5-minute interval numbers yields a characteristic genus-discovery (G-D) curve that reflects the influence of different habitats on patterns of genus discovery.

For example, coral communities in disturbed environments (rock fall areas, reef crests with periodic heavy wave damage) support numerous small coral colonies in mixed assemblages. As the recorder does not need to move far to discover additional genera, there is a rapid initial yield of different corals. The result is a typical exponential G-D curve.

In sheltered environments where coral suffers little disturbance, individual colonies of *Porites* and *Acropora* can grow to extremely large sizes. *Acropora*, in particular, can monopolize vast areas. Here, the search time for different genera is prolonged, yielding a characteristic flat G-D curve. However, if the substrate shows great morphological variation (e.g., spurs, ridges, deep gullies, walls), coral distribution will be patchy. The resulting G-D curve will be noticeably stepped (i.e., there is a rapid initial yield of additional genera in each new habitat followed by a levelling off until the adjacent habitat is reached). The inflection points in this stepped type G-D curve correspond to the points of change from one habitat to another.

The coral assemblages around the Krakatau Islands in Indonesia reflect these three characteristic G-D curves well (Salm, unpublished data; Salm, Sukotjo, Genolagani 1982).

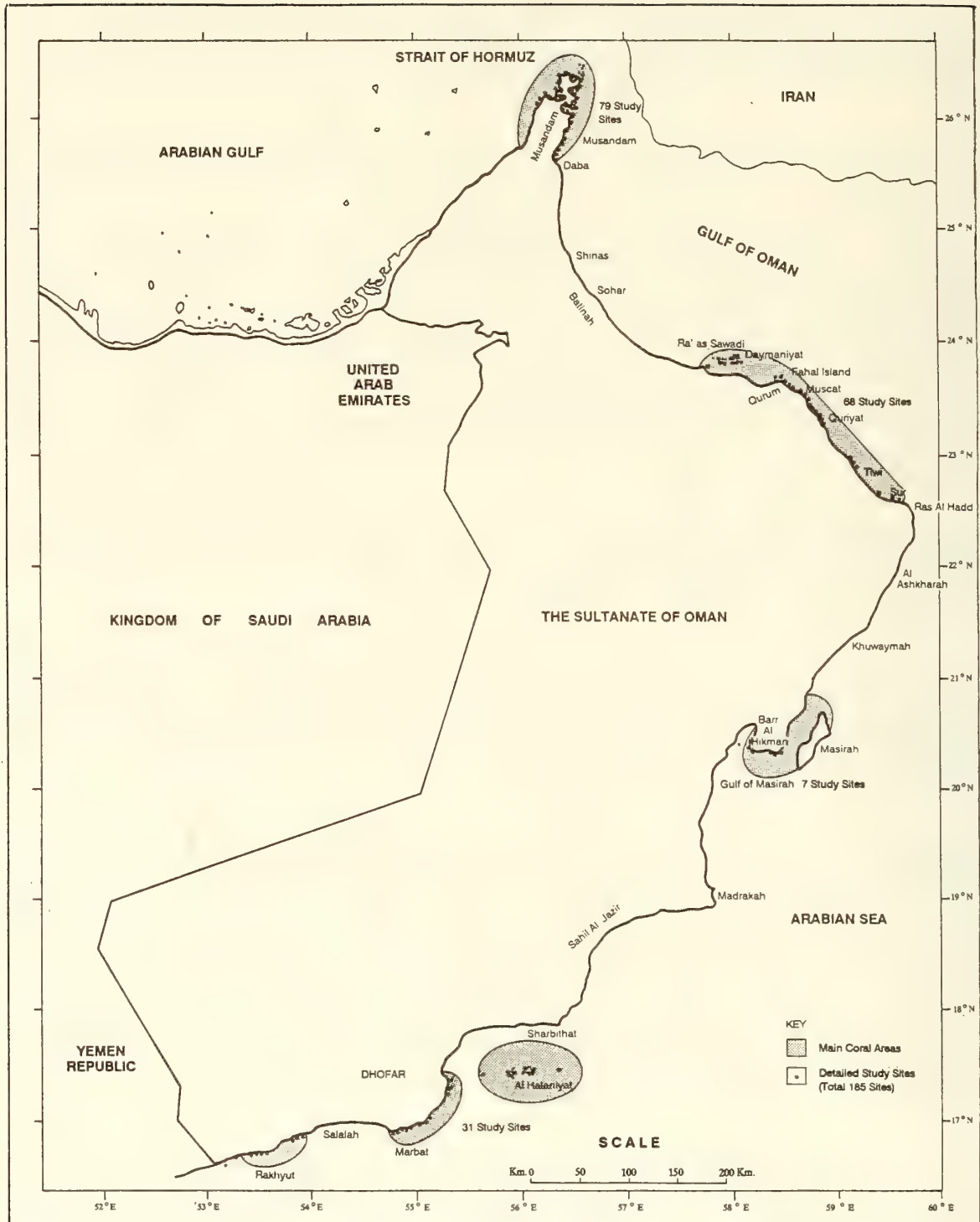


Figure 1. Distribution of coral and coral study sites in Oman

DISTRIBUTION AND NATURE OF CORAL COMMUNITIES

Influences on Coral Occurrence and Growth

Sheppard and Salm (1988) state that only three areas on the mainland support significant coral growth: Musandam, Muscat area and Dhofar. However, it is clear from the coastal zone management studies that major coral growth occurs in four regions in Oman: the Musandam Peninsula and adjacent rocky coast in the north, where coral growth is most prolific; the rocky shores, bays and islands adjacent to the Muscat area, where overall coral diversity is comparable to Musandam but greater at individual sites; the strait west of Masirah Island and adjacent northern Gulf of Masirah, which has the largest areas of continuous coral growth but low diversity; and a number of sheltered bays along mainland Dhofar in the south and the Al Halaniyat Islands offshore, where relict populations of some corals occur that are found nowhere else in the Sultanate. Other parts of the Oman coast either lack corals or support limited growth of small scattered colonies. In some instances the absence of suitable stable substrate precludes the settlement and growth of coral, although seasonal upwelling of cold water, vigorous algal growth, and heavy wave action must also contribute, such as along most of the Arabian Sea coast.

It is interesting that corals had a wider distribution along the Oman coast during Pleistocene times than at present. Beach gravel deposits of this period found from Ra's al Hadd west to beyond Sur contain corals no longer found alive here, but found in Dhofar to the south (*Euphyllia*, *Tubipora*), and a variety of molluscs (*Tridacna maxima*, *Lambis lambis*, *Cypraea rufa*) that are common associates of coral communities elsewhere, but which are no longer found living anywhere in Oman.

There are differences between the corals and coral fishes in the Gulf of Oman and those in the Arabian Sea that appear to be linked to the different oceanographic regimes influencing the coasts north and south of Ra's al Hadd, the eastern point of Oman and the break between the two water masses. During summer, the coast south of Ra's al Hadd bears the brunt of the southwest monsoon winds, swell and upwelling cold water. At this time, sea temperatures reach their highest levels north of Ra's al Hadd.

Complex winds and currents occasionally cause the upwelling of cold water in the Muscat area. This is particularly noticeable in summer when seawater temperatures can drop by as much as 10°C in a day or two. Both summer and winter upwellings are very localized in the Muscat area, and can cause red tides.

The Dhofar upwellings are quite different. These are fairly constant upwellings that continue for 4-5 months during the summer monsoon. This is a period of tremendously rough, cold, green seas when seaweed growth proliferates on all rocky coasts of the southern region. These seaweeds grow fast when upwellings flood the seas with nutrient-rich cool water (16-19°C), some reaching 1.5-2 m in just a few months.

Large patches of dead coral are a common sight and source of speculation in the Muscat area and Musandam. *Acanthaster planci* outbreaks, and temperature-induced bleaching, have killed some coral patches. Entangling fishing nets have destroyed others, and silt-laden flood waters almost certainly contribute to coral death. It is also likely that the summer upwellings contribute to localized coral mortality by sudden large drops in temperature, stressing the corals beyond their limits of tolerance.

The Nature of Corals and Coral Communities

Coral genera found by the CZM Project and other sources are listed in Table 1 for each of the four main coral regions of the Sultanate (Figure 1).

Hard-base corals (those requiring a hard substrate on which to settle and grow) are confined largely to islands, rocky shoals and reefs, and the rocky coasts of Musandam, the Muscat area, the strait west of Masirah Island and northern Gulf of Masirah, and sheltered sections of the Dhofar coast, including the Al Halaniyat Islands (IUCN 1986, 1988, 1989a,b, 1991; Salm 1989; Sheppard & Salm, 1988).

Coral communities tend to be confined to above a maximum depth of 12-18 m, but the percentage cover of live corals drops abruptly below 10 m from 75% or more to less than 40%, and seldom reaches 10% at a depth of 15 m. Certain generally ahermatypic (non reef-building) corals will grow on rocky outcrops down to or deeper than 30 m (*Culicia*, *Balanophyllia*, *Polycyathus*, *Paracyathus*, *Phyllangia*, *Rhizopsammia*, *Leptoseris*). The maximum depth of corals is determined by at least three parameters: the general progression from rock to soft substrate below 12-20 m, the usual presence of a thermocline at 10-15 m (occasionally less) below which the water is both turbid and cold, and the generally murky water. Underwater visibility is unpredictable in the Sultanate, changing daily, and generally less than 10-12 m.

Most corals grow directly on bedrock or on the dead parts of other corals to form a shallow veneer over the underlying substrate. However, conditions favour the build-up of small framework reefs in places. These rudimentary reefs are restricted to sheltered coasts in bays and coves, and along the leeward sides of headlands and islands.

Porites is the dominant builder of framework reefs throughout the Sultanate. Adjacent colonies fuse in the shallows to form flat-topped platforms (reef-flats) that may be settled by other coral species. These fused colonies attain a size of two to four metres in diameter (maximum five metres) along the seaward border of the reef-flat. The large *Porites* colonies and *Porites* dominated reefs probably form the oldest continuously living reefs in the Sultanate.

Pocillopora damicornis commonly forms nearly monospecific banks of living coral to between two and three metres thick. All living corals on some of these rudimentary *P. damicornis* reefs have been extensively or totally killed, and the reefs are being

recolonized by algae, alcyonarians, *Acropora*, *Pocillopora* and other corals.

Montipora foliosa forms large reefs in the northern Gulf of Masirah. *Acropora* and *Hydnophora* may occasionally also form small rudimentary reef patches with a framework 1-2 m thick. In Musandam, *Pavona cactus* and *Montipora* sp. commonly form patches of reef framework more than one metre thick. None of these corals is noted as building framework reefs by Sheppard and Salm (1988).

As noted by Glynn (1983), acroporid reefs were once extensive and widely distributed. Those off the Daymaniyat and Fahal Islands, in Bandar Jissah and at many other sites along the Musandam and Muscat coasts were totally killed, presumably by *A. planci*, but are being recolonized by *P. damicornis*, *Acropora* and other corals.

Coral communities conform to six main types, each of which has a characteristic genus-discovery curve (see p.3 for explanation).

- 1) Rudimentary patch or fringing reefs dominated by *Porites* with few small scattered colonies of other corals (Figure 2A).
- 2) Rudimentary patch reefs dominated by *P. damicornis* with few small scattered colonies of other corals, particularly around the periphery (Figure 2B).
- 3) Rudimentary fringing reefs dominated by tabular and ramose *Acropora* species (Figure 2C).
- 4) Mixed coral assemblages:
 - a) on rudimentary fringing reefs structurally dominated by *Porites* (Figure 3A);
 - b) on rudimentary fringing reefs with a largely obscured underlying framework showing patchy distribution of corals (Figure 3B); and
 - c) covering from 10-99% of the underlying baserock (Figures 3C, 3D).
- 5) Talus banks formed of fragments of dead branching corals (a) with little or no recolonization, (b) in the process of recolonization by the same species, (c) in the process of recolonization by different species.
- 6) Alcyonarians covering rock or dead coral colonies.

It is possible to separate these six coral community types visually based on conspicuous predominance of one or another coral (types 1,2,3,6) that, until closer scrutiny, appears to be the sole genus present. Types 4 and 5 are also clearly visually distinguishable: the former because of the conspicuous abundance of different corals, which is borne out by the rapid yield of coral genera per unit search time (Figures 3A-D); and the latter because of the conspicuous abundance of talus and dead coral colonies.

The genus-discovery curves (G-D curves) for the monogeneric rudimentary reefs level

off rapidly and at low total yield of coral genera (Figure 2A-C). It is interesting that mixed coral assemblages yield similar G-D curves irrespective of the underlying substrate, whether *Porites* reef (Figure 3A), largely obscured reef framework (Figure 3B), or baserock (Figure 3C).

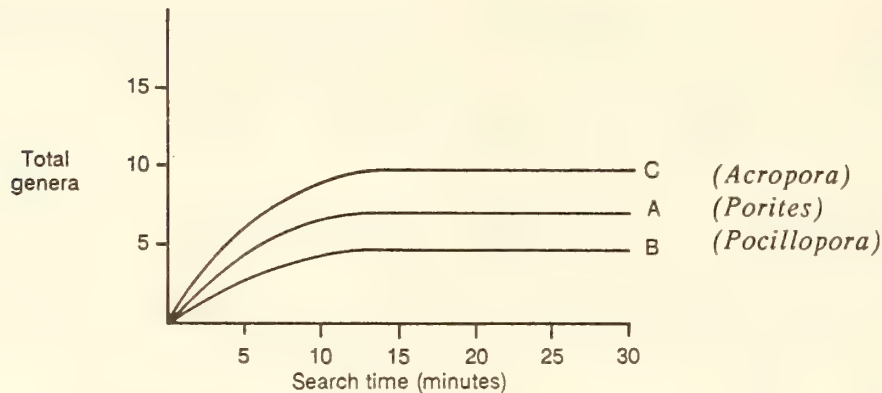


Figure 2. Genus-discovery curves for corals on "monogeneric" reefs.

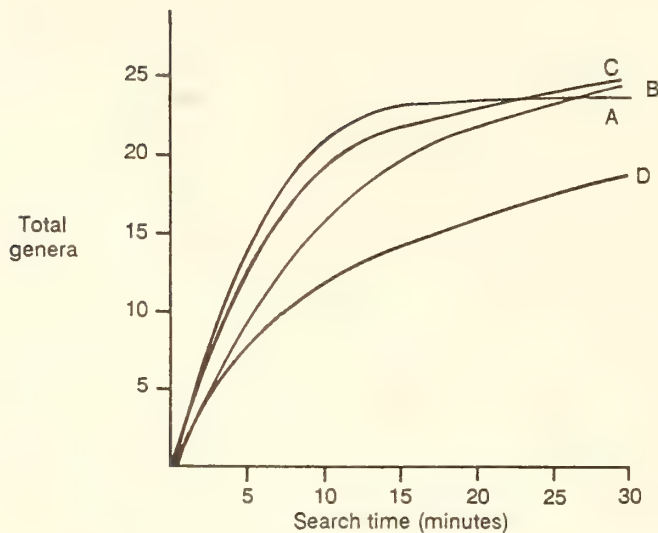


Figure 3. Genus-discovery curves for corals in mixed assemblages (A = *Porites* framework obvious; B = obscured reef framework; C = % cover of baserock >60%; D = % cover of baserock <30%).

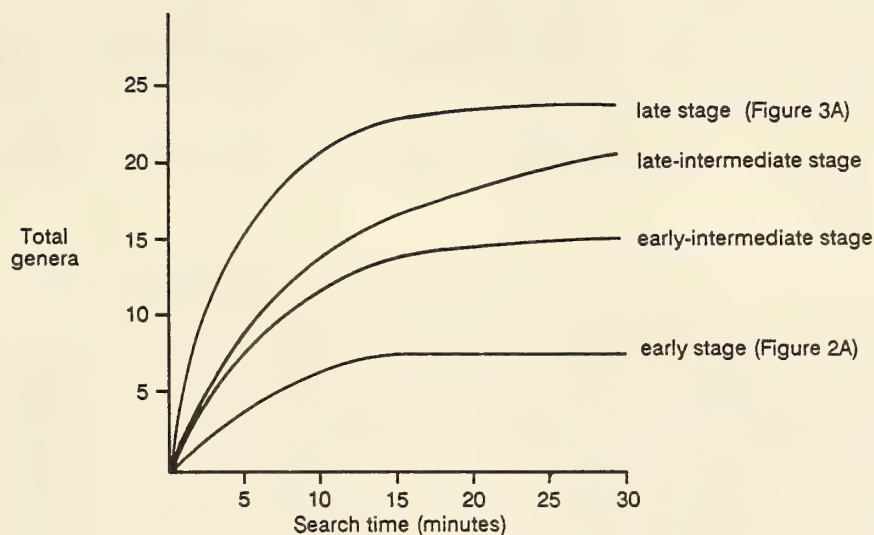


Figure 4. Genus-discovery curves for corals in the primary successional stages of reef development.

The G-D curves support another intuitively obvious observation: mixed coral assemblages with a high percentage cover (more than 60%) yield genera more rapidly per unit search time than those with less than 30% cover (Figures 3C and 3D, respectively). Thus the G-D curve method of recording and displaying coral survey data offers a useful rapid survey tool for classifying coral communities. Its application in this respect merits further investigation.

There is a continuum in G-D curves between those for *Porites* dominated communities (Figure 2A) and mixed assemblage communities (Figure 3). These represent the different stages of reef development. For example:

Early stages of reef development conform to a type 1 community where the substrate is colonized by juxtaposed *Porites* colonies in different stages of fusion with adjacent colonies. This is characterized by a G-D curve with a low rate and total yield of coral genera (Figure 2A).

Intermediate stages of reef development that have *Porites* as the conspicuous structurally dominant coral, but adjacent colonies are fused, flat-topped and dead centrally (micro-atoll form), and colonized by an intermediate variety of corals. These are characterized by G-D curves with genus yield rates and totals intermediate between those

for coral community types 1 and 4a (Figure 4).

Late stages of reef development in which the *Porites* matrix is weakened, colonies die and/or cleave apart providing new hard substrate for colonization by corals (coral community types 4a and 4b). This is the final primary successional stage of reef development (cf. Salm 1976), and is characterized by the highest rate and total yield of coral genera (Figures 3A,B).

Coral Diversity

Rosen (1971) reports 15 coral genera for the Trucial Oman coast and Sawqirah Bay. Green (1983) increased the list to 22 coral genera from the Muscat area, and later revised this list to 28 genera for Oman (Green 1984). The Coastal Zone Management Project increased the Muscat total still further to 42 genera (Salm and Sheppard 1986 Appendix 1), while Sheppard & Salm (1988) present a list of 40 genera. Sheppard (in Sheppard & Salm 1988) produced lists of 38 genera for Musandam and 33 for Dhofar. Additional studies of the Coastal Zone Management Project have increased these totals to 41 and 48 respectively (Table 1, Appendix 1), and increasing the total coral list for the Sultanate from 47 to 53 genera, including the subgenus *Porites* (*Synaraea*), making the list complete or very nearly so (Appendix 1).

However, I have been shown a fungiid coral resembling *Cycloseris* that was allegedly collected from the Raaha area of Dhofar and have been told of other possible sightings, all unconfirmed. Also, two coral genera remain unidentified. Study of the many coral specimens deposited with the Oman Natural History Museum by a coral taxonomist would yield a detailed list of species, possibly including some new to science.

The Fahal Island area has the highest coral diversity (41 recorded genera) of all sites studied in the Sultanate, with all but one genus (*Stylocoeniella*) known from the Muscat area found there. The variety of substrate, depths and exposures to waves and currents in the vicinity of the island are the principal determinants of this high variety of corals, with the deeper rocky outcrops (25-42 m) contributing six additional corals to the total. This is also the type location for the new species *Acanthastrea maxima* Sheppard and Salm 1988, and the site I also first discovered *Parasimplastrea simplicitexta*, a species hitherto only known from fossil specimens from which it was originally described as *Goniastrea simplicitexta* Umbgrove (Sheppard & Salm 1988). However, this new genus is clearly not *Goniastrea* and is closest to *Simplastrea* Umbgrove, hence the derivation of the name *Parasimplastrea*.

As might be expected, coral diversity increases south toward the equator from Musandam (41 genera), which is equivalent to the Muscat area (42 genera) although the composition is a little different, to Dhofar (48 genera). The diversity of corals in the northern Gulf of Masirah is low (27 genera) which probably reflects the isolation of this "island" of coral along a long largely coral-free coast.

The Wildlife and Conservation Area Management Project of the Ministry of Environment has studied corals around Masirah in detail, and likely will increase the number of coral genera for the area. The results of this study are currently not available.

The discovery of additional coral genera for Dhofar in the south shows that coral diversity increases toward the equator. This is counter to the observation by Sheppard and Salm (1988) who described a decrease in diversity from north to south, explaining this phenomenon as a "pseudo-high latitude effect" brought on by seasonal upwelling of cold water and prolific growth of phaeophytes along the southern Dhofar coast.

Coral Communities of Musandam

Almost the entire 600 km of this mountainous, scenic coast is rocky, with its coves, bays, fjordlike inlets, and islands offering extensive hard substrate for coral settlement and growth. The coast is bordered by gradual, stepped, or increasingly steep rocky slopes, or cliffs plunging to great depths. Although coral is not quite as varied as in the Muscat area, it is more abundant and reef development is more substantial. Huge crown-of-thorns starfishes, *A. planci*, are abundant, causing considerable damage to many coral communities of the east and north coasts.

Musandam is formed of two principal components. The Ru'us al Jibal to the south is a prominent mountain complex that rises abruptly from the low sandy plains of the United Arab Emirates. It is joined by a narrow isthmus to the Musandam Peninsula which extends north into the Strait of Hormuz. The Musandam Peninsula is formed of a series of precipitous peninsulas and headlands enclosing deep fjordlike inlets.

The Ru'us al Jibal is generally bordered by shallow sandy seabed along the southeast coast in the Gulf of Oman and the Arabian Gulf coast to the west. Sandy beaches are largely confined to these coasts.

Table 1. List of coral genera by region of Oman

Family	Genus	Musandam	Muscat	Masirah Gulf	Dhofar
Thamnasteriidae	<i>Psammocora</i>	x	x	x	x
Astrocoeniidae	<i>Stylocoeniella</i>	x	x		x
Pocilloporidae	<i>Pocillopora</i>	x	x	x	x
	<i>Stylophora</i>	x	x	x	x
	<i>Seriatopora</i>				*
	<i>Madracis</i>	x	x		x
Acroporidae	<i>Astreopora</i>	x	x	x	x
	<i>Acropora</i>	x	x	x	x
	<i>Montipora</i>	x	x	x	x
Agariciidae	<i>Pavona</i>	x	x	x	x
	<i>Leptoseris</i>		x		x
	<i>Gardineroseris</i>				x
Siderastreidae	<i>Siderastrea</i>	x	x	x	x
	<i>Pseudosiderastrea</i>	x	x	x	x
	<i>Anomastrea</i>	x	x	x	x
	<i>Coscinaraea</i>	x	x	x	x
Poritidae	<i>Porites</i>	x	x	x	x
	<i>Porites (Synaraea)</i>	x	x		
	<i>Goniopora</i>	x	x	x	x
	<i>Alveopora</i>	x		x	x
Faviidae	<i>Favia</i>	x	x	x	x
	<i>Favites</i>	x	x	x	x
	<i>Goniastrea</i>				x
	<i>Platygyra</i>	x	x	x	x
	<i>Leptoria</i>				x
	<i>Montastrea</i>				x
	<i>Plesiastrea</i>	x	x	x	x
	<i>Leptastrea</i>	x	x	x	x
	<i>Cyphastrea</i>	x	x	x	x
	<i>Echinopora</i>	x	x	x	x
Rhizangidae	<i>Culicia</i> ¹	x	x		
	<i>Phyllangia</i> ¹	x	x		x
Oculinidae	<i>Galaxea</i>		x		x
	<i>Parasimplastrea</i>	x	x		x
Merulinidae	<i>Hydnophora</i>	x	x	x	x
Mussidae	<i>Blastomussa</i>	x	x		x
	<i>Symphyllia</i>	x	x		x
	<i>Acanthastrea</i>	x	x	x	x
Pectiniidae	<i>Echinophyllia</i>	x	x	x	x
	<i>Oxypora</i>	x	x		x
Caryophylliidae	<i>Euphyllia</i>				x
	<i>Paracyathus</i> ¹	x	x		x
	<i>Polycyathus</i> ¹	x	x		
	<i>Heterocyathus</i>		x	x	x
	<i>Caryophylliid</i> ¹	x			

Table 1. Continued

Family	Genus	Musandam	Muscat	Masirah Gulf	Dhofar
Dendrophylliidae	<i>Balanophyllia</i> ¹	x	x		
	<i>Rhizopsammia</i> ¹	x			x
	<i>Dendrophyllia</i> ¹	x	x		x
	<i>Tubastraea</i> ¹	x	x		x
	<i>Turbinaria</i>	x	x	x	x
	<i>Heteropsammia</i>		x	x	
Tubiporidae	<i>Tubipora</i> ¹				x
Milleporidae	<i>Millepora</i>				x
Stylasteridae	<i>Stylaster</i> ¹				x
Other	Unidentified 1				x
Other	Unidentified 2				x
TOTAL		41	42	27	48 ²

* *Seriatopora caliendrum* recorded by Sheppard in Sheppard and Salm (1998) is probably *Stylophora pistillata* exhibiting similar growth form.

¹ ahermatypic (azooxanthellate) corals

² total excludes the alcyonarian *Tubipora ?musica* and the two calcified hydrozoans *Millepora*, *Stylaster*.

The coast along the northeast of the Ru'us al Jibal and the Musandam Peninsula falls away rapidly to great depths, often as sheer underwater cliffs. Gravel or cobble beaches are common here, and sandy beaches are few and small. Strong tidal currents scour this coast and eddy in many of the small coves. These current eddies concentrate flotsam and the larvae of marine creatures, both of which have a significant impact on benthic communities.

Limestone cliffs, reaching heights of over 240 m in places, are a major structural component of the coastline covered by this plan, and form 66% (396 km) of its total length. The cliffs are deeply eroded in the intertidal by the combined action of boring organisms (notably the mussel *Lithophaga*) and current scour.

Along most of their length, the cliffs are bordered by seas deeper than six metres with scattered rocky reefs. Elsewhere, the cliffs fall to shallower seas, or an intertidal sand or rock shelf. The well-shaded cliffs suit the growth of flattened sheets of corals that commonly encrust these sheer walls. Among these, Pectinid corals (*Oxypora lacera*, *Echinophyllia aspera*) and *Echinopora* spp. are well represented and, upon closer examination, may yield additional species for Oman.

Rocky shores dominate the coasts bordering wadi fans and beaches in the inner reaches of the fjordlike inlets and other bays, forming about 28.5% of its total length.

These are formed of rock falls, eroded mountain slopes, beach concretions, and wadi fan conglomerates. These rocky shores generally extend underwater as rocky slopes, terraces and outcrops.

Corals are a dominant feature of the Musandam rocky sublittoral, where they form attractive and varied assemblages dominated by a castellated form of *Porites*. The coastal zone management studies have shown reef development to be more prevalent in Musandam than previously suspected by earlier workers (e.g., Cornelius, 1973; Sheppard and Salm, 1988).

There are more reefs in Musandam with true framework development (i.e., a substrate of coral rock that completely obscures the original bedrock) than anywhere else in the Sultanate, and corals are more abundant. True framework reefs were encountered at 73 (66%) of the 111 coral study sites, compared to 43 (61%) for the Muscat area and 17 (30%) for Dhofar.

Porites is the dominant builder of framework reefs. However, *P. damicornis*, *Acropora*, *Montipora*, and *P. cactus* also build small patches of framework reef.

No coral genera specific to Musandam were found, and some obvious genera inexplicably are missing, such as *Leptoseris* and *Galaxea*. While the alcyonarians *Sinularia* and *Sarcophyton* are totally absent from the Arabian Gulf coast of Musandam, and surprisingly sparse elsewhere along most of the rest of the Musandam coast, the brilliant red, orange, yellow or mauve *Dendronephthya klunzingeri*, purple and bushy orange gorgonians, and bright yellow *Antipathes* sp. are notably abundant.

Four coral species that are well represented in Musandam waters are not found elsewhere in the Sultanate. These, which are yet to be identified, include a form of *Pavona* similar to *P. cactus* but with extended leaves resembling *P. decussata*; a fine-branched *Acropora* that forms extensive tangled thickets; a castellated species of *Porites* that is covered by tapering spires; and a "tree"-forming type of *Tubastraea*, sometimes found in very shallow water where the current runs strong.

Coral Communities of the Muscat Area

The exposed north and east facing coasts tend to support relatively small scattered scleractinian coral colonies, and more extensive patches of alcyonarians, chiefly *Sarcophyton*. Percentage cover of living scleractinian corals rarely exceeds 5% of the substrate in these locations.

The leeward west-facing coasts of headlands, southern island shores, and sheltered locations favour the growth of dense coral assemblages (percent cover up to 99%) and framework reefs.

Despite the extensive die-off of acroporid reefs in the Muscat area a number of years ago, there are unaffected *Acropora* communities in two sheltered bays: Bandar Jissah (one small site with discontinuous cover) and Bandar Khayran (three sites). The most extensive site is in Bandar Khayran where two metre diameter tabular *Acropora* colonies with a cover of up to 99% form a rudimentary fringing reef 200 m long.

Other sites where coral growth has continued uninterrupted for a considerable time are the southeast cove of Cemetery Bay, and the small islet in the southeast corner of the large western bay at Bandar Khayran. At the former location individual *Porites* colonies reach diameters of 3-5 m, and those closer to shore have fused to form a flat-topped pavement that is exposed at low tide. At the latter site individual *Porites* colonies reach diameters of three metres and have fused to form a reef-flat that extends more than 100 m west of the islet. "Younger" *Porites* reefs formed of colonies 2-3 m in diameter in various stages of fusion and reef-flat formation are found at many sites among the Daymaniyat islands (Salm 1986a) and in the Bandar Khayran area.

Three sites in the Fahal Island area support unusual coral communities. One includes three rock outcrops near the island in depths of 17-25 m, 20-35 m and 22-42 m. To date, this is the only known location in the Muscat area of three azooxanthellate coral genera (*Phyllangia*, *Rhizopsammia*, *Madracis*). The vertical limestone strata of the mainland peninsula opposite Fahal dip seaward and protrude from the silty substrate as low parallel underwater ridges, forming another site. Where they emerge at a depth of 15 m, they support a number of colonies of the newly described species *Acanthastrea maxima* (Sheppard & Salm 1988). Although isolated colonies of this coral occur elsewhere in Oman, this is the only place where they occur grouped and attain such large calyx (up to 60mm) and polyp size (80-100mm).

The silty substrate between Fahal Island and the mainland is the third site and only location so far that *Heteropsammia cochlea* has been found in Oman. *Heterocyathus aequicostatus* probably also occurs here, but so far has only been found on beaches of the Batinah and central Oman coasts.

Coral Communities of the Gulf of Masirah Area

The west coast of Masirah Island and the Barr al Hikman, separated by a strait to the west, have well developed coral reefs dominated by *Platygyra* and *M. foliosa*. The diversity of corals here is not high, reaching only 27 genera around Barr al Hikman compared to 41 for Musandam, 42 for the Muscat area, and 51 for Dhofar. Between 750 m and 2.3 km off the south coast of Barr al Hikman, and protected by their inaccessibility, lie the largest true coral reefs in the Sultanate. Some of these reefs, which measure many square kilometres, are of further interest because they are built exclusively of *M. foliosa*. Elsewhere in Oman there are few well developed examples of coral reefs, and these are generally small. Coral assemblages covering underlying rock without development of true reef framework are more common. The reefs south of Barr al Hikman form one of the

living natural spectacles of Oman.

Glynn (1987) notes that there are no *Acanthaster* around Masirah Island, suggesting that consequent lack of predation enables the fast growing *Montipora foliosa* to dominate other corals by competitive overtopping, and form large monogeneric stands. During numerous days of study over a six year period, no *Acanthaster* were found on the reefs fringing Barr al Hikman opposite Masirah Island, which also may explain the proliferation of *Montipora foliosa* there into the huge reefs described above.

These remote reefs are unique in the Sultanate from another perspective: the Hikmani tribe who have traditional fishing rights to the area, prohibit all fishing on the reefs for commercial purposes. Fishing is permitted during times of adversity, but for domestic use only. This is a self-enforced community doctrine which effectively maintains the reef as a living cold store.

These hitherto unstudied reefs have many rare and little known species of fishes, and have yielded at least one species new to science: the butterflyfish *Chaetodon dileucos* (Salm & Mee, 1989).

Coral Communities of Dhofar

The mainland coast of Dhofar is approximately 800 km long, stretching from Wadi Haytam on the Jazir coast in the north to Yemen in the south. It includes cliff, rocky and sandy shores. There are numerous small rocky islets close to shore, and the Al Halaniyat Islands (until recently called the Kuria Muria Islands) - the largest group of offshore islands in the Sultanate. Almost the entire coast is seasonally exposed to wave action, ranging from moderate to heavy. Sheltered shores are found in the many coves and larger inlets along the rocky embayed coast between Hasik and the Yemen border.

During summer months, upwellings fuel dense growth of phaeophytes that reach over one metre in length in approximately four months. In the north and central parts there is a mix of *Sargassopsis zamadinii* and *Sargassum* spp., that reach from the intertidal to a depth of about 10 m. In the central part, the kelp *Ecklonia radiata* predominates below this zone to a depth of about 12-15 m. In the south *Sargassum* alone is dominant down to below 12 m. The splash zone of the entire exposed coast is dominated by *Ulva*. These algal communities have been studied in some detail (Barratt 1984). Dhofar is unusual in having dense coral and algal communities growing seasonally in juxtaposition or even in mixed assemblages.

Limestone cliffs are a major structural component of the Dhofar coastline, forming about 25% of its total length. Along most of their length, the cliffs are bordered by seas deeper than six metres with scattered rocky reefs. Elsewhere, the cliffs fall to shallower seas, or to an intertidal sand or rock shelf.

Rocky shores dominate the coast from Hasik to Marbat, and from Mughsayl to the Yemen border, forming about 30% of its total length, and around most of the Al Halaniyat Islands. Rocky reefs fringe most of this coast, providing a substrate for coral and algal communities. The more exposed parts of this coast are fringed by rock pavement covered by algal turf. Algal turfs also carpet many other rocky reefs. These turfs comprise a mixture of different filamentous and smaller algae, and show marked seasonal responses to oceanographic conditions. They may be totally dominated and obscured by macroalgae during the summer season of upwelling. These turf-covered rock pavements are feeding grounds for green and loggerhead turtles.

The sheltered mainland coves and Al Halaniyat Islands support dense coral assemblages and limited framework reefs, growing in unusual association with dense algal growth during the summer monsoon.

The living coral cover generally ranges between less than 0.5% to 80% of the substrate, with levels up to 99% on the reef formations east of Marbat and around the Al Halaniyat Islands. The coastal zone management studies have increased the number of corals known from Dhofar by at least 45% from 33 to 48 coral genera, and have yielded four new records of scleractinian corals for Oman (*Goniastrea pectinata*, *Montastrea curta* and two unidentified genera), and two calcareous species, the alcyonarian *Tubipora ?musica* and the hydrozoan *Millepora*. In addition, true reef development has been documented at 15 new sites, bringing the total of known framework reefs in Dhofar to 17. *Porites* provides the framework for these reefs, which may reach a thickness of three metres. One *Porites* colony measured 12 m in diameter, probably representing more than 1,000 years growth, and is the largest such colony so far discovered in the Sultanate.

Porites supports dense seasonal breeding concentrations of the spiny lobster *Panulirus homarus* in at least four sites, and shallow rocky reefs attract smaller concentrations in at least two sites.

Certain of the Dhofar corals, fishes, seaweeds, starfishes, and sea urchins are not found elsewhere in Oman. For example, the coral communities include at least five scleractinian genera (*Euphyllia fimbriata*, *G. pectinata*, *M. curta*, *Leptoria phrygia*, *Gardineroseris planulata*), one alcyonarian genus (*Tubipora*), and two hydrozoan genera (*Millepora*, *Stylaster*) that are found only in Dhofar, and the fishes include at least three butterflyfishes (*Chaetodon lunula*, *Chaetodon auriga*, *Megaprotodon strigangulus*), and the newly described *Amphiprion omanensis* Allen & Mee 1991, that are absent or uncommon elsewhere in Oman.

Sandy beaches are a major component of the Dhofar coast, and occupy 40% of its total length, while gravel/cobble beaches form about 5%. Small ephemeral beaches form and erode along parts of the coast. The seabed off the beaches is shallow and sandy with flat rocky reefs subject to heavy sand scour during the rough summer monsoon.

THREATS TO CORAL COMMUNITIES

Reef growth is interrupted in Oman by episodic coral mortality. This appears to be confined to corals in more exposed locations. But the pattern of die-off is confusing, as the damage may affect only parts of a reef or one in a series of adjacent coral patches.

All that remains of former reef development at the die-off sites are large dead *Porites*, *Platygyra* or *Symphyllia* colonies, the stumps of once large tabular *Acropora*, or talus banks formed of dead *P. damicornis* or *Acropora*.

Large patches of dead coral are common in the Muscat area and Musandam, but not the Masirah area or Dhofar. Some areas have been killed by the crown-of-thorns starfish *A. planci*, others by entangling fishing nets, and damage to corals by the anchors of fishermen and divers remains a problem on many reefs.

A white patch disease, where necrotic coral tissue sloughs rapidly off colonies of *Platygyra* exposing the white skeleton beneath, is prevalent in parts of Musandam, and appears to be a significant cause of mortality for the genus. No invasion of coral tissue by pathogens is visible *in situ*, and tissue specimens were not collected for further study.

Collapse of coastal limestone cliffs undercut by the boring mussel *Lithophaga* and wave scour destroys coral colonies, as noted by Glynn (1983). However, this phenomenon does not explain die-offs in areas far from cliffs or signs of recent rock falls, such as along the southern shores of the Daymaniyat Islands.

Episodic massive discharge of silt-laden flood waters into the sea certainly would destroy corals in affected areas. However, this phenomenon is more likely to explain the absence of reef formations than the die-off patterns. It is unlikely to have any effect on corals of the Daymaniyat Islands which lie 18-20 km offshore.

Temperature stress is another likely cause of coral mortality and its effect on reef development in Oman requires study. The sudden chilling of surface water during summer is well-known among the diving community. Summer is a period of unpredictable and localized upwelling in the Muscat area. Cells of cold upwelling water drawn by winds or currents over a coral community would cause a precipitous drop in temperature of many degrees centigrade. Green (pers. comm.) has noted a drop in surface seawater temperature of 15°C over 14 days in July 1983, and regular monthly fluctuations of as much as 8°C during summer (Green 1983). Cold water upwelling is known to cause coral bleaching and mortality, with areas prone to these events having few, small and young reefs (Glynn, 1990) - a condition that fits coral communities of the Sultanate. If temperature stress proves to be a cause of coral mortality, it would help explain the disjunct pattern of die-off, death of large *Porites* and *Symphyllia* colonies, and dead corals in areas swept by currents near deep water.

Temperature-induced bleaching and mortality of corals is a definite problem. Coral bleaching in the summer of 1990 caused some corals to die in the Muscat area, but killed up to 95% of the corals shallower than three metres on reefs in Musandam.

The pattern of coral community development and die-off is a product of all above parameters. Recreational diving is a more recent cause of coral damage (Salm 1986b), but its effects are currently localized and relatively slight.

Of the 239 coral communities described for Musandam, Muscat and Dhofar (Appendix 2), at least 162 (68%) are damaged by fishery activities, litter and *A. planci* predation. Musandam has the highest incidence of damage (93 sites, 84% of the study sites in Musandam), followed by the Muscat area with 48 sites (68% of study sites there), and Dhofar (24 sites, 37% of total Dhofar sites).

Bioerosion of damaged or dead corals has a serious impact on development of reef framework, and follows the pattern described by Glynn (1988) in the eastern Pacific. The principal agents of bioerosion include boring algae, sponges, the mussel *Lithophaga*, and the echinoids *Diadema setosum*, *Echinothrix diadema*, and *Echinometra mathaei*. *Diadema* forms the densest accumulations, massing on talus areas around the bases of live coral colonies.

Fishery Related Damage to Coral Communities

There is a considerable amount of dead and broken coral in Musandam and the Muscat area. Fishing activity certainly contributes to this. Gill nets, fish traps, and anchors are dropped directly onto reefs of branching coral species, breaking them, and frequently becoming entangled. If these cannot be broken free, they are abandoned *in situ*, and contribute to further coral damage. Monofilament net, the use of which is prohibited in Oman, is especially damaging to marine life when abandoned on the seabed. Use of monofilament nets is increasing in the Sultanate, and few villages are without them. One such net examined in Musandam yielded a number of live fishes, crabs and lobsters among many more that were dead. Ropes, gill nets and fish traps entangled in and damaging corals were recorded at 60 (54%) sites studied underwater in Musandam, 43 (61%) in the Muscat area and, 20 (35%) in Dhofar.

Patches of *P. damicornis* and *Acropora* spp. are particularly vulnerable to damage from abandoned fishing nets. The nets entangle and break off coral branches which roll up in them. A net weighted in this way and still partly supported by floats can bounce and drag over coral, leaving a swathe of dead rubble. Around the Daymaniyat Islands, 25-80% of some *P. damicornis* patches have been destroyed in this way. Although nets were found to kill part or all of the corals they entangled, this still would not explain the pattern of complete die-off, especially in areas lacking any sign of nets or physical damage to corals.

Litter abounds underwater in Musandam. Plastic bags, fabric and the ballast bags of Iranian small boat traders are especially damaging to corals which they envelop and smother. In sheltered coves where fishermen careen their boats for maintenance work, sheets of linoleum and plastic, paint cans and other rubbish are snagged in corals. At least 12 (30%) coral sites examined showed considerable damage attributable to fishermen and these traders; at one site alone, more than 120 pairs of trousers (part of an Iranian consignment) were seen caught in and smothering coral. Thirty-one (28%) of the coral sites viewed suffered from litter damage caused by fishermen alone. Between their litter and fishery activity, fishermen caused damage to corals at 80 (72%) of the 111 study sites in Musandam. The extent of pollution in this remote and beautiful area is stunning and tragic.

The quantity of litter underwater attributable to fishermen is far less in the Muscat area (7 sites, 10%) and Dhofar (6 sites, 11%) than Musandam. The combined effect of fishery activity and litter damages coral at 43 sites (61%) in the Muscat area, and 20 sites (35%) in Dhofar. There are many other sites in Oman where nets are entangled on the substrate, threatening benthic invertebrate communities, fishes, spiny lobsters, dolphins and turtles.

The Sultanate is concerned about the environment, but only now is becoming aware of the damage beneath the seas. Five years ago a large underwater clean-up was sponsored by the Ministry of Commerce and Industry through the Tourism Department. Eighty five divers took part in this two day event, pulling up more than three tons of old fishing nets. This has been followed by two recent clean-up campaigns inspired and organized by the Intercontinental Hotel in collaboration with the Ministry of Environment. These two clean-ups yielded tons more fishing nets and other rubbish from the seabed, and were well supported by many concerned divers. Among the victims dead in these nets were many crabs, fishes and lobsters, and one green turtle.

Acanthaster planci

The distribution of *A. planci* in Oman appears to be restricted to the Gulf of Oman and the Strait of Hormuz. During the course of the seven-year CZM study, none was found along the Arabian Sea or Arabian Gulf coasts of Oman. These observations agree with those of Glynn (1983) who carried out a dedicated survey for the species.

However, Glynn (1983) found no *Acanthaster* in 12 sample sites in Musandam that he visited in 1982. Eleven of these sites were along the Arabian Gulf coast where the CZM studies showed the starfish to be absent in 1989/90, and one site was in Khawr Kumzar in the north where there was a profusion of *Acanthaster* in 1989/90. Because of the localized nature of the crown-of-thorns outbreaks, it is possible that Glynn simply missed the starfish in Khawr Kumzar, if indeed they were there.

A. planci is a major cause of coral destruction in Musandam. Severe infestations

associated with large patches of dead coral where found at 57 (51%) of the locations studied underwater by the CZM project, all on the north and east coasts. No *Acanthaster* were found on the west coast. The largest infestation was found off Jazirat Habalayn where 117 starfishes were counted in 15 minutes off the south side of the island. Sheppard (1986) makes no mention of *Acanthaster* at this site four years previously.

Also in 1986, Zahuriyin in Khawr Habalayn had a new infestation in an area of luxuriant table coral *Acropora*, with 27 *A. planci* seen exposed in 0.4 hectare (Salm, 1986c). Based on a visual estimate, the starfishes had killed 25% of the *Acropora* community. By 1990, this same site was reduced to a wasteland of dead and broken coral with very limited recolonization along the deep edge of the former coral band.

Currents eddy in the many small coves along the mountainous Musandam coast and around islands, concentrating flotsam which eventually sinks and explains the abundance of litter underwater there. These current eddies also would concentrate coral and *A. planci* larvae (hence better coral settlement and growth and higher coral predation there), helping to explain the numerous, small, disjunct concentrations of *A. planci*.

Many of these coves are found below steep valleys at the confluences of cliffs or precipitous mountain faces. Rainwater and mud runoff at these sites is high and concentrated by eddies which heighten their effect on corals. Perhaps this localized runoff effect and high *A. planci* predation combine to cause episodic mass mortality of vulnerable corals and to explain the high incidence of dead coral and talus banks in many coves.

Table 2. Corals eaten by *Acanthaster planci* in Oman

Psammocora sp.
Stylophora pistillata
Pocillopora damicornis
Acropora spp.
Montipora spp.
Porites spp.
Goniopora sp.
Pavona cactus
Platygyra daedalea
Cyphastrea serailia
Echinophyllia aspera

Glynn (1983) concludes that recurring outbreaks of crown-of-thorns starfish, *A. planci*, may have a large influence on the development of coral communities in the Muscat area. However, as Glynn points out, *Acanthaster* is a fairly selective feeder, which generally avoids colonies of *Pocillopora*, *Porites* and *Symphyllia* (although it regularly does feed on both *Pocillopora* and *Porites* in Oman). Thus, it is unlikely that starfish predation alone would cause the extensive mortality of large colonies or patches of these three corals.

In Oman, *A. planci* was seen to feed on a variety of hard corals (Table 2) and the alcyonarian *Dendronephthya klunzingeri*, but never *Symphyllia*, and clearly preferred species of *Acropora*.

Glynn (1987) notes that commensal crustacean guards render pocilloporid reefs apparently resistant to *Acanthaster* predation, even when at outbreak densities, which may explain the prevalence of *Pocillopora* patches in many areas where other corals are largely dead.

A. planci was relatively common in the Muscat area, being seen at 20 (28%) study sites, but never in concentrations equivalent to those of Musandam. The vast coral-free sandy coast at Ra's al Hadd (the breakpoint between the Gulf of Oman and the Arabian Sea), and the pattern of northerly currents sweeping up to this point from the south with easterly currents moving offshore to the north, possibly prevent the southerly drift of *A. planci* larvae and its invasion of Arabian Sea coral communities from the north. The pattern of seasonal upwelling and low seawater temperatures (16-19°C) along the south coast of Oman may well prevent invasion from that direction, as cool water is known to inhibit development of *Acanthaster* larvae (Glynn 1983).

Coral Bleaching in the Sultanate of Oman

Coral bleaching is the loss of colour that accompanies an expulsion of the symbiotic zooxanthellae (microscopic plankton living in the coral tissue). It was described by Vaughan as long ago as 1914, and was first recognized to result from elevated seawater temperatures by Yonge and Nichols (1931). Recently, and undoubtedly in response to increasing concern among scientists about global warming, coral bleaching has been the focus of considerable field and laboratory study, leading to the general conclusion that elevated sea water temperatures coupled with UV radiation are the chief agents responsible for coral bleaching (cf. Brown 1990).

Coral bleaching in the Sultanate of Oman was noticed first by divers who expressed concern that corals were "dying" on the reefs off Marjan Beach, the public beach at Ra's al Hamra. Subsequent investigation of the area showed that there had been extensive bleaching of corals there, giving the impression that the corals were in fact dead.

Certain interested divers were briefed on coral bleaching and asked to report their observations. It was clear that bleaching was widespread throughout the Muscat area,

where sea water temperatures had reached as high as 39°C in June 1990.

Field work undertaken through the IUCN Coastal Zone Management Project, was extended to investigate coral bleaching in Musandam, certain reefs being monitored from June through October 1990.

Coral bleaching and related mortality has not been recorded previously from the Sultanate of Oman. The amount of dead coral and lack of framework reef development, despite apparently suitable conditions, may well be attributable to past bleaching events.

Coral Bleaching in the Muscat Area

On 29 June 1990, sea water temperature at "Cat Island" off the Marine Science and Fisheries Centre reached 39°C. There was reportedly extensive bleaching of corals surrounding the islet. When visited in September 1990, the corals had largely recovered. At that time the seawater temperature was 24°C down to a depth of four metres and up to 500 m off the island. *Symphyllia* was the only scleractinian coral to show residual signs of bleaching, whereas all colonies of the alcyonarian coral *Sinularia* in exposed locations remained bleached to a pale yellow colour.

The Marjan Beach area was first visited in July 1990 in response to reports of widespread coral mortality there. At that time the water temperature was 28°C, and no mortality was recorded although many colonies of the following corals were severely bleached: *Montipora* and *Porites*, which are the most abundant corals, and *Acropora* which is less common in the area. The *Acropora* and some *Montipora* colonies were bleached pure white, and the *Porites* had turned very pale blue, mauve, brown or yellow.

Symphyllia, *Favia*, *Hydnophora microconos*, *Turbinaria*, *Stylophora*, *Goniopora*, and *Acanthastrea echinata*, were less severely bleached, retaining a yellow or yellow-brown colour, and all *Platygyra* were totally unaffected. The soft corals *Sinularia* and *Sarcophyton*, and great numbers of zoanthids also were severely bleached to very pale yellow. Many of the zoanthids were already dead, showing no reaction to touch and partly floating free.

The bleaching was confined to the inner reaches of the bay. By early September, the faviids, *Porites*, and *Montipora* had all regained normal colouration, and mortality appeared to be slight (<2% of all corals) and confined to colonies of *Acropora*.

Reports of extensive bleaching around Fahal Island and in Bandar Khayran were received from divers who regularly visit the areas. There was no sign of this bleaching by mid-October at Fahal Island, and there appeared to be no bleaching-related mortality. In early November, the only sign of bleaching at Bandar Khayran was pale yellow-green *Sinularia* in shallow exposed locations.

Coral Bleaching in Musandam

In July 1990 two sites were investigated for coral bleaching: Jazirat Habalayn in Khawr Habalayn, and Jazirat Maqlab in Khawr Ash Shamm. The findings prompted follow-up monitoring of these sites in August and October, and the study of additional sites. Appendix 3 presents observations at these sites.

Coral bleaching was more severe in the large fjordlike bays than outside along open coasts. The temperatures were higher in these environments (e.g., August temperature ranges surface to 10 m: Khawr Habalayn 35-32°C; Khawr Ash Shamm 34-33°C) than in the well-flushed straits (Khawr Quway' 32-31°C; Ra's Rarak in the southern Strait of Hormuz 32-30°C) where there was no bleaching.

Bleaching and related mortality were most severe between the surface and three metres depth. Mortality varied from <1% (Khawr Quway') to >95% (Gulf of Oman coast, patches in Khawr Ash Shamm). The principal species affected were branching *Acropora* (Khawr Ash Shamm), *Stylophora*, *Acropora* and *Platygyra* (Khawr Habalayn), and table *Acropora* (Gulf of Oman coast).

Bleaching and related mortality may explain the enigma of the many hollowed-out live *Platygyra daedalea* colonies in the bays and fjords of Musandam. Observations at Maqaqah, following severe bleaching of *Platygyra*, show that dead patches are rapidly covered by silt and invaded by algae. This opens the way for numerous boring organisms to penetrate and hollow out the coral colony, including the conspicuous sea urchins *Echinometra* and *Diadema*. This rapid bioerosion of corals appears to be an important factor inhibiting the development of more framework reefs in Musandam.

Although the sea temperatures reached higher levels in the Muscat area, temperatures higher than 30°C were not sustained for as long as they were in Musandam. Sea temperatures in the Muscat area characteristically show great variability during summer, rising during periods of calm still weather and dropping rapidly in response to upwellings of cold water. Green and Keech (1986) report a drop in temperature at 10 m depth from 32°C to 17°C in less than 14 days in July 1983. During 1990, surface water temperatures dropped more rapidly, cooling from 39°C at the end of June to 24°C in less than one week. The Musandam sea temperatures reached 34-35°C and remained above 30°C down to a depth of 10 m for at least three months in the areas of greatest coral mortality.

Glynn *et al.* (1988) and Glynn (1990) report that the highest mean percent coral mortality in the eastern Pacific occurs in areas with normally lower and more variable sea water temperatures, and the lowest mortality occurs in areas with normally high and stable temperatures. However, the length of exposure to elevated temperatures is a key determinant of coral bleaching (Jokiel and Coles 1990) and, as the Oman examples show, of coral mortality. For example, the Muscat area, with greatly varying sea water temperatures, had shortest exposure to elevated temperatures and least coral mortality (<2%). The high temperature (39°C) was enough to induce bleaching, but the exposure

apparently was too short to be lethal.

In Musandam, corals in straits with strong currents and well mixed cooler water experienced least mortality (<1%), presumably because exposure to elevated temperatures was too short. It could be argued that the pattern observed by Glynn *et al.* (1988) and Glynn (1990) applies elsewhere in Musandam. For example, corals in the large fjordlike bays suffered lower mortality *presumably* because water circulation is lower and temperatures remain stable at higher levels than in the small open bays on the east coast where coral mortality in the upper three metres exceeded 95%, and where *presumably* water circulation is greater, and temperatures generally lower and more variable. Unfortunately, baseline current and temperature data do not exist for these remote sites.

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APPENDIX 1. CORAL LISTS (coordinates from National Survey Authority Map Series K6611, 1:100,000; for full names of corals see Table 1; Unid = unidentified genus; G = total genera; S = total species; numbers of species listed in columns)

Site	Site Name	Map Coordinates	Psam	Styloc	Poc	Stylop	Ser	Mad	Ast	Acr	Monti	Pav	Leptos	Gar	Sid
001	Ra's al Jirri N	DQ190015-220040	0	0	1	1	0	0	0	3	2	0	0	0	0
002	Cove 1, RSM	DQ198022	0	0	0	0	0	0	0	2	1	0	0	0	0
003	Khawr Idah S	DQ200026	0	0	1	1	0	0	0	3	2	0	0	0	0
004	Shaykh Mas'ud W	DQ214041	0	0	1	0	0	0	0	2	1	0	0	0	0
005	Ra's Salti Ali	DP237994	1	0	1	1	0	0	0	3	1	0	0	0	0
006	Ra's Shakhs	DP280997-284998	1	0	1	0	0	0	0	4	1	0	0	0	0
007	Khawr ash Shamm	DP340980	1	0	1	1	0	1	0	4	2	4	0	0	1
008	Jazirat Maqlab	DP344974	1	0	1	1	0	1	0	4	2	3	0	0	0
009	Maksar	DP395980	1	0	0	1	0	0	0	3	0	4	0	0	1
010	Jazirat Sibi	DQ394004	1	0	0	1	0	0	0	3	0	2	0	0	0
011	Ghassah	DQ320026	1	0	1	1	0	0	0	4	1	1	0	0	0
012	Khawr Ghubb Ali	DQ350060	1	0	1	1	0	1	0	4	1	1	0	0	1
013	Khawr Ghubb Ali	DQ324075	1	0	1	1	0	0	0	4	1	1	0	0	1
014	Khawr Ghubb Ali	DQ368060	1	0	1	0	0	0	0	3	1	1	0	0	0
015	Umm al Ghanam	DQ344126	1	0	1	1	0	0	0	3	0	2	0	0	1
016	Umm al Ghanam	DQ356167	0	0	1	1	0	0	0	2	2	1	0	0	0
017	Umm al Ghanam	DQ363170-366167	1	0	1	1	0	0	1	4	2	2	0	0	1
018	Umm al Ghanam	DQ361163-360152	1	0	1	1	0	0	0	3	2	1	0	0	0
019	Umm al Ghanam	DQ358132-352127	0	0	1	1	0	0	0	3	2	1	0	0	0
020	Khawr al Quway'	DQ374169	1	0	1	1	0	0	0	2	1	1	0	0	0
021	Ra's Rarak	DQ386174	1	0	1	1	0	0	0	2	1	2	0	0	0
022	Khawr Khayran	DQ390160	0	0	1	1	0	0	1	4	2	1	0	0	0
023	Khawr Ran	DQ410164-414169	1	0	1	1	0	0	1	4	1	1	0	0	0
024	Jazirat Abu Sir	DQ420182	1	0	1	1	0	0	0	4	1	2	0	0	0
025	Jazirat Abu Sir	DQ418174	0	0	1	0	0	0	0	3	1	1	0	0	0
026	Khawr Kumzar	DQ417156-416148	0	0	1	1	0	0	1	2	1	1	0	0	0
027	"Salla"	DQ432147-440146	1	0	1	1	0	0	1	2	2	1	0	0	0
028	Khawr Ma'ili	DQ442146-440132	2	0	1	1	0	0	1	2	2	1	0	0	0
029	Jazirat al Khayl S	DQ449165-462160	1	0	1	0	0	0	0	2	2	2	0	0	0
030	Ghubbat al Khouse	DQ480130	1	0	1	1	0	0	1	4	3	2	0	0	1
031	Ghubbat al Khouse	DQ462126-460115	1	0	1	1	0	0	1	3	1	2	0	0	0
032	Ghubbat al Khouse	DQ500118	1	0	1	0	0	0	0	1	0	1	0	0	0
033	Ghubbat al Khouse	DQ490137	0	0	1	1	0	0	0	4	3	2	0	0	1
034	Ghubbat al Khouse	DQ478145	1	0	1	1	0	0	0	3	1	2	0	0	1
035	Jazirat Bu Rashid	DQ495204	1	0	1	1	0	0	0	3	2	1	0	0	0
036	Jazirat Musandam	DQ525176	1	0	1	1	0	0	0	2	3	1	0	0	0
037	Jazirat Musandam	DQ526184	0	0	1	1	0	0	0	2	1	0	0	0	0
038	Jazirat Musandam	DQ535165	0	0	1	1	0	0	0	2	2	1	0	0	0
039	Jazirat Musandam	DQ517156	1	0	1	1	0	0	0	4	2	1	0	0	1
040	Dawhat ash Shisah	DQ440060	1	1	1	1	0	0	1	4	2	2	0	0	1
041	Dawhat ash Shisah	DQ404080	1	0	1	0	0	0	1	2	2	1	0	0	0
042	Dawhat ash Shisah	DQ410055	0	0	1	1	0	0	1	2	1	1	0	0	0
043	Dawhat ash Shisah	DQ411028	0	0	1	1	0	0	0	3	0	1	0	0	0
044	Dawhat ash Shisah	DQ425016	0	1	1	0	0	0	1	4	1	2	0	0	1
045	Dawhat ash Shisah	DQ462018	0	0	1	0	0	0	1	3	0	1	0	0	1
046	Khaysah-Bashin	DQ494017-487968	1	0	1	0	0	0	0	3	2	1	0	0	0
047	Ra's Khaysah S	DQ476004	1	0	1	0	0	0	1	2	1	0	0	0	0
048	Ra's Bashin S	DQ485968	0	0	1	1	0	0	0	4	2	2	0	0	1
049	Umm al Fayyarin	DP548955	0	0	1	1	0	0	0	2	1	1	0	0	0
050	Ghubbat Shabus	DQ460960	1	0	1	1	0	0	1	3	2	2	0	0	1
051	Ghubbat Shabus	DP440957	1	0	1	1	0	0	1	2	2	2	0	0	1

APPENDIX 1. Continued

Site	Pseud	Ano	Cos	Por	P(Syn)	Gonio	Alv	Favia	Favit	Gonia	Pla	Leptor	Monta	Ples	Lepta	Cyph	Echin	Cul	Phy	Gal	Par	Hyd
001	0	1	0	1	0	1	0	0	2	0	1	0	0	0	1	1	0	0	0	0	0	0
002	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0
003	0	1	0	1	0	1	0	0	2	0	1	0	0	0	1	1	0	0	0	0	0	0
004	0	1	0	1	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0
005	0	0	0	2	0	1	0	2	0	0	2	0	0	0	1	2	0	0	0	0	0	1
006	0	0	0	1	0	0	0	2	0	0	1	0	0	0	2	1	0	0	0	0	0	0
007	1	1	1	2	0	1	0	4	1	0	2	0	0	1	2	1	0	0	0	0	0	0
008	1	1	1	2	0	1	0	3	1	0	2	0	0	1	2	1	0	0	0	0	0	0
009	0	0	1	1	0	0	0	4	1	0	2	0	0	1	2	1	0	0	0	0	0	0
010	0	0	1	1	0	0	0	4	1	0	2	0	0	0	1	1	0	0	0	0	0	0
011	0	0	0	2	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0
012	0	1	1	3	0	1	0	2	2	0	2	0	0	1	2	1	1	0	0	0	0	1
013	0	1	1	3	0	1	0	2	2	0	2	0	0	1	2	1	1	0	0	0	0	1
014	0	0	1	1	0	0	0	2	1	0	1	0	0	0	1	1	0	0	0	0	0	0
015	1	1	0	1	0	1	0	2	2	0	1	0	0	1	2	2	1	0	0	0	0	2
016	0	1	1	2	0	1	0	3	1	0	2	0	0	0	2	1	0	0	0	0	0	2
017	1	1	1	2	0	2	0	3	2	0	2	0	0	0	2	2	1	0	0	0	0	2
018	1	1	1	2	0	1	0	0	2	0	2	0	0	0	1	0	1	0	0	0	0	1
019	0	1	0	3	0	1	0	2	3	0	2	0	0	0	1	1	1	0	0	0	0	0
020	1	1	1	2	0	1	0	3	1	0	2	0	0	0	1	1	0	0	0	0	0	1
021	0	1	1	1	0	1	0	2	2	0	1	0	0	1	2	1	1	0	0	0	0	2
022	1	1	1	3	0	3	0	3	1	0	2	0	0	0	2	2	1	0	0	0	0	2
023	1	1	1	1	0	2	0	2	2	0	1	0	0	1	3	2	1	0	0	0	0	2
024	1	1	1	3	0	1	0	2	2	0	2	0	0	0	0	1	1	0	0	0	0	2
025	0	0	0	1	0	0	0	1	2	0	1	0	0	0	2	1	1	0	0	0	0	2
026	0	1	1	1	0	2	0	2	1	0	2	0	0	0	1	1	1	0	0	0	0	1
027	1	1	1	1	0	1	0	1	2	0	2	0	0	0	2	1	1	0	0	0	0	2
028	0	1	1	1	0	1	0	1	2	0	2	0	0	0	2	2	1	0	0	0	0	0
029	1	0	1	1	1	2	0	1	2	0	1	0	0	1	1	1	1	0	0	0	0	2
030	1	1	1	1	0	2	0	2	1	0	1	0	0	1	3	1	1	0	0	0	1	2
031	0	0	1	1	0	2	0	0	1	0	1	0	0	0	1	1	1	0	0	0	1	1
032	0	0	0	1	0	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0
033	1	1	1	2	0	2	0	2	1	0	1	0	0	1	3	1	1	0	0	0	1	2
034	1	0	1	2	0	1	0	1	1	0	2	0	0	0	2	2	1	0	0	0	0	1
035	1	1	1	1	0	2	0	3	3	0	1	0	0	1	3	0	1	0	0	0	0	2
036	0	0	0	1	0	1	0	1	1	0	1	0	0	1	1	1	1	0	0	0	0	2
037	0	0	0	1	0	1	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	1
038	0	0	0	2	0	1	0	1	2	0	1	0	0	0	0	0	1	0	0	0	0	1
039	0	0	1	1	0	1	0	1	2	0	1	0	0	0	1	1	1	0	0	0	0	2
040	1	1	1	2	0	2	0	2	2	0	3	0	0	1	3	2	1	0	0	0	1	2
041	0	1	1	1	0	1	0	1	2	0	2	0	0	0	1	1	1	0	0	0	0	1
042	0	0	1	1	0	2	0	1	2	0	1	0	0	0	2	1	1	0	0	0	1	2
043	0	0	0	2	0	1	0	0	1	0	2	0	0	0	2	0	1	0	0	0	1	1
044	1	1	1	2	1	2	0	2	3	0	3	0	0	1	3	2	1	0	0	0	0	2
045	0	0	1	1	0	1	0	1	3	0	2	0	0	1	0	0	1	0	0	0	0	2
046	0	1	0	1	0	2	0	1	1	0	2	0	0	0	3	1	1	0	0	0	0	2
047	0	0	1	2	0	1	0	1	2	0	1	0	0	0	2	1	1	0	0	0	1	2
048	0	1	1	2	0	1	0	1	3	0	2	0	0	0	2	1	1	0	0	0	1	2
049	1	0	1	1	0	1	0	1	1	0	1	0	0	1	1	0	1	0	0	0	0	0
050	1	1	1	2	0	2	0	1	3	0	2	0	0	1	2	1	2	0	0	0	1	2
051	0	1	1	1	0	1	0	1	2	0	2	0	0	1	2	1	2	0	0	0	1	1

APPENDIX 1. Continued

Site	Bla	Sym	Aca	Echinoph	Oxy	Euph	Parac	Poly	Heteroc	Cary	Bal	Rhiz	Den	Tub	Tur	Heterop	Tubip	Mille	Stylas	Unid	G	S
001	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	16
002	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	10
003	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	16
004	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	12
005	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	20
006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	14
007	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	23	36
008	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	21	32
009	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	25
010	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	19
011	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	16
012	0	1	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	26	35
013	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	23	32
014	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	15
015	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	28
016	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	26
017	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	26	40
018	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	19	25
019	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	16	25
020	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	24
021	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	24	30
022	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	23	37
023	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	25	35
024	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	22	32
025	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	16	21
026	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	24
027	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	23	29
028	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	28
029	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	27
030	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	29	40
031	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	25
032	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	14
033	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	27	39
034	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	29
035	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	24	35
036	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	23
037	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	15
038	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	19
039	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	20	26
040	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	30	45
041	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	24
042	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	22	27
043	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	16	21
044	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	27	42
045	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	20	26
046	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	27
047	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	26
048	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	24	35
049	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	20	21
050	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	30	42
051	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	29	34

APPENDIX 1. Continued

Site	Site Name	Map Coordinates	Psam	Styloc	Poc	Stylop	Ser	Mad	Ast	Acr	Monti	Pav	Leptos	Gar	Sid
052	Ghubbat Shabus	DP475925-480916	1	0	1	1	0	0	1	3	2	1	0	0	1
053	Ra's Dillah N	DP486909	0	0	1	0	0	0	0	2	1	0	0	0	0
054	Khawr Habalayn	DP400900	2	1	1	1	0	0	1	5	2	2	0	0	1
055	Khawr Habalayn	DP474906-473911	1	0	1	0	0	0	1	4	2	1	0	0	1
056	Khawr Habalayn	DP425911	1	0	1	1	0	0	1	4	2	1	0	0	0
057	Khawr Habalayn	DP414950	0	0	1	1	0	0	0	4	1	1	0	0	1
058	Khawr Habalayn	DP395977	1	0	0	1	0	0	0	3	1	3	0	0	1
059	Khawr Habalayn	DP357938	0	0	1	1	0	0	1	5	1	2	0	0	1
060	Khawr Najd	DP340903	1	0	0	0	0	0	0	3	1	2	0	0	0
061	Khawr Habalayn	DP420850	2	1	1	0	0	0	1	4	2	2	0	0	1
062	Khawr Habalayn	DP430854	1	0	1	1	0	0	1	4	2	0	0	0	0
063	Dawhat Qabal	DP400800	0	0	0	1	0	0	0	2	0	1	0	0	0
064	Dawhat Qabal	DP415782	0	0	1	1	0	0	0	3	1	1	0	0	0
065	Ra's Marovi	DP430743	1	0	1	1	0	0	0	4	2	2	0	0	1
066	Ma'awi	DP404731	1	0	1	1	0	0	1	4	2	1	0	0	0
067	Limah	DP425700	0	0	1	1	0	0	0	3	1	2	0	0	0
068	Ghubbat Aqabah	DP400670	1	0	1	1	0	0	0	2	1	1	0	0	0
069	Ghubbat Aqabah	DP437677-424680	1	0	1	1	0	0	0	2	1	1	0	0	0
070	Ghubbat Aqabah	DP395649	0	0	0	1	0	0	0	1	0	1	0	0	0
071	Massar	DP375604	0	0	1	1	0	0	0	4	2	1	0	0	0
072	Musandam SE	DP382589	1	0	1	0	0	0	0	3	2	1	0	0	0
073	Musandam SE	DP369563	0	0	1	1	0	0	0	4	2	1	0	0	0
074	Sanat	DP357543	0	0	1	1	0	0	0	4	2	0	0	0	0
075	Dawhat Haffah	DP310480	1	0	0	0	0	0	0	2	0	1	0	0	0
076	Zaghi S	DP276416	1	0	1	1	0	0	0	3	1	2	0	0	1
077	Ra's Sawt N	DP279410	1	0	1	1	0	0	0	4	1	2	0	0	0
078	Daba	DP272400	1	0	0	1	0	0	0	4	1	2	0	0	0
079	Zaghi	DP282327	0	0	1	1	0	0	0	2	1	3	0	0	0
080	Ra's Sawadi	FM798311	1	0	1	1	0	0	0	2	1	1	0	0	0
081	Daymaniyat (Gnl)	EM967380-200370	2	1	1	1	0	0	1	2	3	2	0	0	1
082	Daymaniyat	EM967380	1	0	1	0	0	0	1	1	1	1	0	0	0
083	Daymaniyat	EM987366	1	0	1	0	0	0	1	1	2	1	0	0	0
084	Daymaniyat	FM000364	1	0	1	1	0	0	1	1	2	1	0	0	0
085	Daymaniyat	FM001364	0	0	1	1	0	0	0	1	1	1	0	0	0
086	Daymaniyat	FM076384-093387	3	1	1	1	0	0	1	2	3	2	0	0	0
087	Daymaniyat	FM076384	2	1	1	0	0	0	0	2	2	1	0	0	0
088	Daymaniyat	FM077384	1	0	1	1	0	0	0	2	3	1	0	0	0
089	Daymaniyat	FM090387	1	0	1	1	0	0	1	2	2	2	0	0	0
090	Daymaniyat	FM090385	1	0	1	1	0	0	0	2	1	1	0	0	0
091	Daymaniyat	FM103386-112390	1	0	1	1	0	0	0	2	2	2	0	0	0
092	Daymaniyat	FM106390	1	0	1	1	0	0	0	2	2	2	0	0	0
093	Daymaniyat	FM111386	1	0	1	1	0	0	0	2	2	1	0	0	0
094	Daymaniyat	FM116393-131391	3	0	1	1	0	0	1	2	3	2	0	0	1
095	Daymaniyat	FM118388	1	0	1	1	0	0	0	1	1	0	0	0	0
096	Daymaniyat	FM116394	1	0	1	1	0	0	1	0	1	2	0	0	0
097	Daymaniyat	FM126387	2	0	1	1	0	0	1	2	3	2	0	0	1
098	Daymaniyat	FM134394-143395	3	1	1	1	0	0	1	2	3	2	0	0	0
099	Daymaniyat	FM143395	2	1	1	1	0	0	1	1	2	2	0	0	0
100	Daymaniyat	FM150360	2	0	1	0	0	0	1	3	1	2	0	0	0
101	Daymaniyat	FM190367-200370	1	0	1	1	0	0	1	2	2	1	0	0	0
102	Daymaniyat	FM194371	1	0	1	1	0	0	1	2	2	1	0	0	0
103	Fahal Island (Gnl)	FM530195	2	0	1	1	0	1	1	2	2	2	1	0	1
104	Fahal Island	FM530194	2	0	1	1	0	0	1	2	1	1	0	0	0
105	Fahal Island W	FM529195	2	0	0	1	0	0	1	1	1	2	0	0	1

APPENDIX 1. Continued

Site	Pseud	Ano	Cos	Por	P(Syn)	Gonio	Alv	Favia	Favit	Gonia	Pla	Leptor	Monta	Ples	Lepta	Cyph	Echin	Cul	Phy	Gal	Par	Hyd
052	1	0	1	2	0	2	0	1	3	0	2	0	0	1	2	1	1	0	0	0	1	2
053	0	0	0	2	0	1	0	1	3	0	3	0	0	0	3	1	0	0	0	0	0	1
054	1	1	1	4	0	2	0	4	2	0	3	0	0	1	3	1	1	1	0	0	1	2
055	0	1	0	4	0	1	0	4	2	0	2	0	0	1	2	1	1	0	0	0	1	2
056	0	0	0	4	0	1	0	3	1	0	2	0	0	0	1	0	1	0	0	0	0	2
057	0	0	1	1	0	0	0	3	2	0	2	0	0	0	2	1	1	0	0	0	0	0
058	0	0	1	2	0	1	0	3	1	0	2	0	0	1	3	1	0	0	0	0	0	1
059	0	1	1	3	0	1	0	3	0	0	2	0	0	1	2	1	1	0	0	0	1	1
060	0	0	1	1	0	1	0	2	1	0	1	0	0	0	1	1	1	0	0	0	0	1
061	1	0	1	1	0	1	0	2	2	0	1	0	0	1	2	1	1	1	0	0	1	2
062	0	0	1	3	0	2	0	1	2	0	3	0	0	1	1	0	1	0	0	0	1	2
063	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
064	0	1	1	3	0	2	0	2	2	0	2	0	0	1	2	2	1	0	0	0	1	2
065	0	1	1	2	1	2	0	1	3	0	2	0	0	0	2	1	1	0	0	0	1	2
066	0	1	1	2	1	1	0	3	3	0	2	0	0	1	2	2	1	0	0	0	1	2
067	0	0	0	1	0	1	0	1	1	0	2	0	0	0	0	1	1	0	0	0	0	0
068	0	0	1	2	0	2	0	0	2	0	2	0	0	0	2	1	1	0	0	0	0	1
069	0	0	1	2	0	2	0	0	2	0	2	0	0	0	2	1	1	0	0	0	0	1
070	0	0	0	2	0	0	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0
071	1	1	1	2	0	1	0	3	3	0	2	0	0	0	3	1	1	0	0	0	0	2
072	1	1	1	3	0	2	0	2	2	0	2	0	0	1	1	1	1	0	0	0	0	1
073	0	0	0	3	0	1	0	2	2	0	3	0	0	1	1	1	1	0	0	0	0	2
074	0	0	0	3	0	1	0	2	1	0	1	0	0	0	1	1	1	0	0	0	0	0
075	0	0	1	2	0	0	0	1	1	0	2	0	0	0	0	1	0	0	0	0	0	0
076	1	1	1	3	0	2	0	3	2	0	2	0	0	1	2	1	1	0	0	0	0	2
077	1	1	1	2	0	1	0	3	3	0	2	0	0	1	3	2	1	0	0	0	0	1
078	0	1	1	1	0	1	0	2	3	0	2	0	0	0	2	1	1	0	0	0	0	0
079	1	1	1	1	0	1	1	3	3	0	2	0	0	1	2	1	1	0	0	0	1	1
080	0	1	1	2	0	1	0	1	3	0	1	0	0	0	1	1	0	0	0	0	0	1
081	1	1	2	3	0	2	0	1	3	0	1	0	0	1	3	2	2	1	0	1	1	2
082	0	0	1	1	0	1	0	1	1	0	1	0	0	1	1	0	0	0	0	0	0	0
083	0	0	1	1	0	1	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0
084	0	0	1	2	0	1	0	0	1	0	1	0	0	1	1	0	1	0	0	1	0	1
085	0	0	0	2	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
086	0	0	1	2	0	2	0	2	2	0	1	0	0	1	3	1	0	1	0	1	1	1
087	0	0	0	2	0	2	0	1	2	0	1	0	0	1	2	1	0	0	0	0	0	0
088	0	0	0	2	0	2	0	0	2	0	1	0	0	1	2	1	0	0	0	0	1	1
089	0	0	1	2	0	1	0	2	2	0	1	0	0	1	1	1	0	0	0	1	0	1
090	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
091	0	0	0	2	0	2	0	1	2	0	1	0	0	1	1	1	0	0	0	1	0	1
092	0	0	0	1	0	2	0	1	1	0	1	0	0	1	1	1	0	0	0	1	0	1
093	0	0	0	2	0	1	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	1
094	0	0	1	2	0	2	0	1	2	0	2	0	0	1	2	1	0	1	0	1	1	1
095	0	0	0	1	0	0	0	1	0	0	2	0	0	0	1	1	0	0	0	0	0	1
096	0	0	1	1	0	2	0	1	2	0	1	0	0	1	1	1	0	0	0	1	1	1
097	0	0	1	2	0	2	0	1	2	0	1	0	0	0	2	1	0	1	0	0	0	1
098	0	0	2	2	0	1	0	1	2	0	1	0	0	1	3	1	1	0	0	0	1	1
099	0	0	2	1	0	1	0	1	2	0	1	0	0	1	3	1	1	0	0	0	1	1
100	1	1	2	1	0	2	0	1	3	0	1	0	0	1	2	2	1	1	0	0	1	1
101	0	0	1	2	0	1	0	1	2	0	1	0	0	1	2	1	1	0	0	0	0	1
102	0	0	1	1	0	1	0	1	2	0	1	0	0	1	2	1	0	0	0	0	0	1
103	1	1	2	2	0	2	0	2	4	0	1	0	0	1	1	1	1	1	1	1	1	1
104	0	1	0	2	0	1	0	1	4	0	1	0	0	1	0	1	0	0	0	0	0	1
105	0	1	1	1	0	1	0	2	3	0	1	0	0	1	0	1	1	1	0	1	0	1

APPENDIX 1. Continued

Site	Bla	Sym	Aca	Echinoph	Oxy	Euph	Parac	Poly	Heteroc	Cary	Bal	Rhiz	Den	Tub	Tur	Heterop	Tubip	Mille	Stylas	Unid	G	S
052	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	26	36
053	0	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	16	24
054	1	2	1	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	31	53
055	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	25	39
056	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	20	31
057	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	20	28
058	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	31
059	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	34
060	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	22
061	1	2	1	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	28	40
062	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	22	33
063	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	10
064	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	34
065	0	1	1	1	1	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	26	39
066	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	25	38
067	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	19
068	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	21	27
069	0	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	21	27
070	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	11
071	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	34
072	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	24	33
073	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	29
074	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	22
075	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	12
076	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	25	37
077	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	24	37
078	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	19	28
079	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	25	34
080	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	20	24
081	2	1	1	1	1	0	0	1	0	0	0	0	1	1	3	0	0	0	0	0	34	53
082	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	17	17
083	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	16
084	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	19	21
085	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	11	12
086	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	29	41
087	1	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	19	26
088	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	18	25
089	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	22	28
090	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	12
091	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	22	28
092	0	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	21	25
093	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	15	18
094	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	26	37
095	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	12	13
096	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	22	25
097	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	23	32
098	1	1	0	1	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	26	38
099	1	1	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	26	33
100	0	1	1	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	28	38
101	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	20	26
102	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	19	23
103	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	0	0	41	52
104	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	20	26
105	1	1	1	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	29	34

APPENDIX 1. Continued

Site	Site Name	Map Coordinates	Psam	Styloc	Poc	Stylop	Ser	Mad	Ast	Acr	Monti	Pav	Leptos	Gar	Sid
106	Fahal, Shallow Rf	FM536199	2	0	0	0	0	1	0	0	2	1	1	0	0
107	Fahal, Deep Reef	FM535206	0	0	0	0	0	1	0	0	0	0	1	0	0
108	Ra's al Hamra N	FM527162	0	0	0	0	0	0	0	0	0	0	0	0	1
109	Darsayt	FM580148	1	0	1	1	0	0	0	2	1	0	0	0	0
110	Aint East	FM588146	3	0	1	1	0	0	0	2	1	1	0	0	0
111	Kalbuh	FM617136	1	0	1	1	0	0	0	3	2	1	0	0	0
112	Muscat Island E	FM632137	1	0	1	0	0	0	0	1	0	0	0	0	0
113	Muscat Island	FM634132	1	0	1	1	0	0	0	1	1	1	0	0	0
114	Cemetary Bay	FM633122	0	0	2	2	0	0	0	3	1	2	0	0	0
115	Cemetary Bay	FM635119	1	0	1	1	0	0	0	2	0	1	0	0	0
116	Cemetary Bay	FM637121	2	0	1	1	0	0	1	2	0	1	0	0	0
117	Cemetary Bay S	FM638117	0	1	0	0	0	0	0	1	0	0	0	0	0
118	Cat Island	FM642092	1	0	1	1	0	0	1	2	1	2	0	0	0
119	Al Bustan	FM653075	1	0	1	1	0	0	1	2	1	1	0	0	1
120	Qantab	FM668068	1	0	1	1	0	0	1	2	1	2	0	0	0
121	Jissah (Gnl)	FM685060	2	0	1	1	0	0	1	2	1	2	0	0	1
122	Jissah	FM676064	0	0	1	1	0	0	1	2	1	0	0	0	0
123	Jissah	FM682056	0	0	1	1	0	0	0	2	0	0	0	0	0
124	Jissah	FM684057	0	0	1	0	0	0	1	1	1	1	0	0	1
125	Jissah	FM686053	1	0	1	1	0	0	0	2	0	0	0	0	0
126	Jissah	FM687050	1	0	1	1	0	0	0	2	1	1	0	0	0
127	Khayran (Gnl)	FM770025	2	1	1	1	0	0	1	6	2	2	1	0	1
128	Khayran	FM757029	1	0	1	1	0	0	1	2	1	2	0	0	0
129	Khayran	FM758022	1	0	1	1	0	0	1	6	1	1	0	0	0
130	Khayran	FM760022	1	0	1	1	0	0	0	2	1	1	0	0	0
131	Khayran	FM762023	1	0	1	1	0	0	1	4	2	2	0	0	1
132	Khayran	FM783026	0	0	1	1	0	0	0	1	1	0	0	0	0
133	Khayran	FM784024	1	0	1	1	0	0	1	1	0	2	0	0	0
134	Khayran	FM784021	1	0	0	1	0	0	1	2	2	2	0	0	0
135	Ra's Khayran	FM792014	1	0	1	1	0	0	1	1	1	1	0	0	0
136	Ra's Khayran	FM794014	2	0	1	1	0	0	1	2	2	2	0	0	0
137	Ash Shaykh S	FM796006	1	0	1	1	0	0	1	2	1	0	0	0	0
138	Ash Shaykh SE	FM798008	1	0	1	1	0	0	1	2	1	1	1	0	0
139	As Sifah N	FL816972	0	0	1	0	0	0	0	1	1	0	0	0	0
140	As Sifah	FL844885	0	0	1	1	0	0	1	2	1	0	0	0	0
141	Ra's Abu Da'ud	FL960800	2	0	1	1	0	0	1	2	2	2	0	0	0
142	Bimmah N	GL185450	0	0	0	0	0	0	1	3	1	0	0	0	0
143	Makalla Wabar	GL293304	2	0	1	0	0	0	1	3	2	1	0	0	0
144	Ra's N Qalhat	GL380185	1	1	1	0	0	0	1	2	1	1	0	0	0
145	Bi'r Bira' W	GL520045	2	0	1	1	0	0	1	3	3	1	0	0	1
146	Bi'r Bira'	GL533033	1	0	1	1	0	0	1	2	1	1	0	0	0
147	S Shiya	GK755959	2	0	1	0	0	0	1	2	2	0	0	0	1
148	Barr al Hikman	FH520520	1	0	1	1	0	0	0	2	3	1	0	0	0
149	Barr al Hikman	FH480500	0	0	0	1	0	0	0	1	3	0	0	0	0
150	Barr al Hikman	FH420528	0	0	0	1	0	0	0	1	2	0	0	0	0
151	Ra's Kanasah	FH270530	0	0	0	1	0	0	0	1	0	1	0	0	0
152	Ra's Shajrit	FH244594-246600	0	0	0	1	0	0	0	1	1	0	0	0	1
153	Jazirat Abb	FH215672	0	0	0	0	0	0	0	1	0	0	0	0	1
154	Gulf of Masirah	FH300480	1	0	1	1	0	0	1	2	3	1	0	0	1
155	Bandar Qinqari E	BD891827-890812	0	0	0	1	0	0	1	2	2	1	0	1	0
156	Wadi Bayt Said E	BD828795	1	0	0	1	0	0	0	3	2	1	1	1	0
157	Wadi Aingalf E3	BD756770	1	0	0	1	0	0	0	1	2	3	1	1	1
158	Wadi Aingalf E2	BD752769	2	0	0	1	0	0	0	2	2	1	0	1	0
159	Wadi Aingalf E1	BD748767	1	0	0	1	0	0	0	2	2	2	1	1	0

APPENDIX 1. Continued

Site	Pseud	Ano	Cos	Por	P(Syn)	Gonio	Alv	Favia	Favit	Gonia	Pla	Leptor	Monta	Ples	Lepta	Cyph	Echin	Cul	Phy	Gal	Par	Hyd
106	1	1	2	1	0	2	0	1	1	0	1	0	0	1	1	1	0	0	0	0	1	0
107	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
108	1	1	1	1	0	1	0	3	2	0	1	0	0	1	0	0	0	0	0	0	1	1
109	0	1	1	1	0	0	0	1	2	0	1	0	0	0	1	1	0	0	0	0	0	1
110	0	1	1	2	0	1	0	1	3	0	1	0	0	1	2	1	0	0	0	0	1	1
111	0	1	0	2	0	1	0	0	2	0	2	0	0	0	2	0	0	0	0	0	0	1
112	0	0	0	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1
113	0	1	1	1	0	1	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	1
114	0	0	0	2	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	0
115	0	0	0	2	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
116	1	1	1	2	0	2	0	0	2	0	2	0	0	1	2	1	0	1	0	0	1	0
117	0	1	0	1	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
118	1	1	2	2	0	2	0	1	2	0	1	0	0	1	2	1	0	0	0	0	1	1
119	0	1	1	1	0	2	0	0	2	0	1	0	0	1	1	1	1	0	0	0	0	1
120	0	1	1	1	0	2	0	1	2	0	1	0	0	1	1	1	1	0	0	1	0	1
121	1	1	1	2	0	2	0	3	2	0	1	0	0	1	3	1	1	1	0	1	1	1
122	0	1	1	1	0	2	0	1	2	0	1	0	0	1	3	1	1	0	0	0	0	1
123	0	0	0	2	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
124	1	1	1	2	0	2	0	2	1	0	1	0	0	1	1	1	0	0	0	0	1	0
125	0	0	0	1	0	1	0	1	1	0	1	0	0	0	1	1	0	0	0	1	0	1
126	0	0	0	2	0	1	0	3	1	0	1	0	0	0	1	1	1	0	0	1	0	1
127	1	1	2	2	0	2	0	2	3	0	1	0	0	1	3	2	1	0	0	1	1	1
128	0	1	1	1	0	2	0	1	3	0	1	0	0	1	2	2	1	0	0	0	0	1
129	0	1	1	2	0	1	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0	1
130	0	1	1	1	0	1	0	2	1	0	1	0	0	1	1	1	1	0	0	0	0	1
131	1	1	2	2	0	1	0	2	3	0	1	0	0	1	2	2	1	0	0	0	1	1
132	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1
133	0	1	0	2	0	2	0	0	1	0	1	0	0	1	1	1	1	0	0	1	1	1
134	0	1	0	1	0	1	0	1	2	0	1	0	0	0	1	1	0	0	0	0	0	1
135	0	0	0	2	0	1	0	0	1	0	1	0	0	0	1	0	1	0	0	1	0	1
136	0	1	1	2	0	2	0	2	2	0	1	0	0	1	3	1	1	0	0	0	0	1
137	0	0	1	2	0	1	0	1	2	0	1	0	0	1	0	0	0	0	0	0	0	1
138	0	1	2	1	0	1	0	1	1	0	2	0	0	0	2	2	0	0	0	0	1	1
139	0	0	0	1	0	1	0	2	1	0	1	0	0	1	1	1	0	0	0	0	0	1
140	0	0	0	1	0	1	0	1	2	0	1	0	0	0	0	1	0	0	0	0	0	1
141	1	1	1	1	0	1	0	1	2	0	1	0	0	1	1	1	0	0	0	0	2	2
142	1	1	1	2	0	2	0	2	2	0	2	0	0	1	2	1	0	0	0	0	1	0
143	1	1	1	2	0	2	0	1	3	0	1	0	0	1	1	1	0	0	0	0	1	1
144	1	1	1	1	0	2	0	1	1	0	1	0	0	1	3	1	0	0	0	0	1	1
145	1	1	1	3	0	3	0	2	3	0	2	0	0	1	2	1	0	0	0	1	1	1
146	0	1	0	2	0	2	0	1	1	0	1	0	0	0	2	0	0	0	0	1	1	1
147	1	1	1	1	0	1	0	1	2	0	1	0	0	0	3	0	0	0	0	0	1	1
148	0	0	1	2	0	2	0	3	3	0	2	0	0	1	1	0	0	0	0	0	0	2
149	1	0	1	3	0	0	0	2	4	0	2	0	0	0	1	1	0	0	0	0	0	0
150	0	0	0	2	0	1	0	2	3	0	1	0	0	0	0	1	0	0	0	0	0	2
151	1	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	2
152	1	1	2	3	0	2	1	3	4	0	3	0	0	1	1	1	1	0	0	0	0	2
153	1	1	0	1	0	0	0	1	3	0	1	0	0	0	0	0	0	0	0	0	0	0
154	1	1	2	3	0	2	1	3	4	0	3	0	0	1	3	1	1	0	0	0	0	2
155	1	0	1	0	0	1	0	2	3	0	1	0	0	1	1	1	0	0	0	0	1	2
156	0	0	1	1	0	1	0	1	3	0	2	0	0	1	1	1	0	0	0	0	1	2
157	0	0	1	3	0	0	0	2	4	0	2	1	0	0	1	1	1	0	0	1	0	2
158	0	0	1	1	0	2	0	2	4	0	1	1	0	1	0	1	0	0	0	0	0	2
159	0	0	1	0	0	2	0	2	5	0	2	0	0	1	2	1	1	0	0	0	0	2

APPENDIX 1. Continued

Site	Bla	Sym	Aca	Echinoph	Oxy	Euph	Parac	Poly	Heteroc	Cary	Bal	Rhiz	Den	Tub	Tur	Heterop	Tubip	Mille	Stylas	Unid	G	S
106	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	20	24
107	0	0	0	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	10	10
108	0	0	1	1	1	0	0	0	0	0	1	0	0	1	2	1	0	0	0	0	19	23
109	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	18	20
110	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	22	29
111	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	17	24
112	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	13	13
113	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	22	22
114	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	15	21
115	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	10
116	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	25	32
117	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	12	12
118	0	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	25	33
119	0	1	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	23	27
120	0	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	25	30
121	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	30	40
122	0	1	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	21	27
123	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	9	11
124	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	24	27
125	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	16	17
126	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	21	25
127	1	1	2	1	1	0	1	0	0	0	0	0	1	1	2	0	0	0	0	0	34	53
128	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	24	31
129	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	22	28
130	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	22	24
131	0	1	2	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	27	41
132	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	12	12
133	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	22	25
134	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	20
135	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	19	20
136	1	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	26	36
137	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	17	20
138	1	1	1	0	1	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	25	31
139	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	16	17
140	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	16
141	1	1	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	25	33
142	1	1	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	19	29
143	1	1	1	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	24	34
144	1	1	1	1	1	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	27	33
145	1	1	2	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	27	44
146	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	19	23
147	0	1	1	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	20	28
148	0	0	2	1	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	18	32
149	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	21
150	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	11	17
151	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	9	11
152	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	20	35
153	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	10
154	0	0	2	1	0	0	0	0	1	0	0	0	0	0	3	1	0	0	0	0	27	47
155	0	0	2	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	21	28
156	0	0	1	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	23	40
157	1	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	25	37
158	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	20	29
159	0	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	22	35

APPENDIX 1. Continued

Site	Site Name	Map Coordinates	Psam	Styloc	Poc	Stylop	Ser	Mad	Ast	Acr	Monti	Pav	Leptos	Gar	Sid
160	Wadi Aingalf E	BD746773	1	0	0	1	0	0	0	2	2	2	1	1	0
161	Raaha E	BD664749	0	0	0	1	0	0	0	4	2	2	0	1	0
162	Raaha W	BD663747	0	0	0	1	0	0	1	2	2	2	1	0	0
163	Raaha	BD654743	0	0	0	1	0	0	0	2	2	2	0	1	0
164	Jazirat Hino W	BD594755	0	0	1	1	0	0	0	1	1	0	0	0	0
165	Ra's Marbat	BD530786	2	1	0	1	0	1	0	1	2	1	2	1	0
166	Ra's Raysut	ZU208749	0	0	0	1	0	0	0	0	0	0	0	1	0
167	Rock Stack	ZU190740	0	0	0	1	0	0	0	1	1	1	0	1	0
168	Ra's Hamar	ZU140710	0	0	0	1	0	0	0	1	1	0	0	1	0
169	Fizayih	YU892631-888625	0	0	0	1	0	0	0	1	1	0	0	1	0
170	Ghubbat Fizayih W	YU846574-850584	0	0	0	0	0	0	0	0	0	0	0	0	0
171	Millepora Bay	YU710544	0	0	0	1	0	0	0	3	3	2	0	1	0
172	Ma'alqawt	YU700546-693548	0	0	0	1	0	0	0	1	1	0	0	0	0
173	Kharfot	YU488508	0	0	0	0	0	0	0	0	1	0	0	1	1
174	Hallaniyah (Gnl)	CE960360	0	0	1	1	0	1	0	3	3	3	1	0	1
175	Hallaniyah NW	CE900364	0	0	1	1	0	0	0	2	3	3	0	0	1
176	Hallaniyah SE	DE032355	0	0	0	1	0	0	0	3	1	0	0	0	0
177	Hallaniyah S2	CE929338	0	0	0	1	0	1	0	3	3	2	1	0	0
178	Hallaniyah SW	CE911342	0	0	0	1	0	0	0	2	2	0	0	0	0
179	Hallaniyah SW	CE911342	0	0	0	1	0	0	0	2	1	1	0	0	0
180	As Sawda (Gnl)	CE780350	1	0	0	2	0	0	1	3	3	3	1	0	0
181	As Sawda NE	CE808346	0	0	0	1	0	0	1	2	2	0	1	0	0
182	As Sawda E	CE808334	1	0	0	2	0	0	0	3	3	2	1	0	0
183	As Sawda S	CE781336	0	0	0	2	0	0	1	3	3	3	0	0	0
184	As Sawda NW	CE760350	0	0	0	1	0	0	0	3	1	0	0	0	0
185	Dhofar (Gnl)		2	1	1	1	1	1	1	4	3	3	2	1	1

APPENDIX 1. Continued

Site	Pseud	Ano	Cos	Por	P(Syn)	Gonio	Alv	Favia	Favit	Gonia	Pla	Leptor	Monta	Ples	Lepta	Cyph	Echin	Cul	Phy	Gal	Par	Hyd
160	0	0	1	0	0	2	0	2	5	0	2	0	0	1	2	1	1	0	0	0	0	2
161	0	0	1	1	0	1	0	1	3	0	2	0	0	0	1	1	1	0	0	1	0	1
162	0	0	1	3	0	1	0	1	3	0	2	0	0	0	0	1	1	0	0	1	0	1
163	1	0	1	1	0	1	0	1	3	0	2	0	0	1	1	1	1	0	0	0	0	2
164	0	0	1	3	0	1	0	2	2	0	2	0	0	1	0	1	1	0	0	0	0	2
165	1	0	1	0	0	1	0	2	3	0	1	0	0	1	1	1	0	0	0	0	0	0
166	0	0	2	0	0	1	0	1	2	0	0	0	0	0	1	0	0	0	0	0	0	0
167	1	0	1	0	0	0	0	1	1	0	1	0	0	0	2	1	0	0	0	0	0	2
168	1	0	1	1	0	1	0	1	2	0	1	0	0	1	1	1	0	0	0	0	1	0
169	1	0	0	3	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
170	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
171	0	1	1	1	0	1	0	1	3	0	2	0	0	1	0	1	1	0	0	0	0	2
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
173	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0
174	1	1	1	3	0	2	1	3	3	1	2	1	0	1	2	3	1	0	0	1	1	2
175	1	1	1	3	0	2	0	3	2	0	1	1	0	1	1	1	1	0	0	1	1	2
176	0	1	0	3	0	1	1	1	3	0	1	1	0	0	1	1	0	0	0	0	0	1
177	1	0	1	3	0	2	0	3	2	1	1	1	0	1	2	3	1	0	0	1	0	1
178	0	0	0	3	0	1	0	1	2	0	1	1	0	0	1	0	0	0	0	1	0	0
179	1	0	1	3	0	2	1	2	2	0	2	1	0	0	2	1	1	0	0	1	1	2
180	1	1	1	4	0	2	1	4	3	1	2	1	0	1	1	2	1	0	0	1	1	2
181	0	1	1	2	0	2	1	2	2	0	1	1	0	1	1	0	1	0	0	1	1	2
182	0	1	1	2	0	1	0	3	2	0	1	1	0	0	1	2	1	0	0	1	0	2
183	1	0	1	4	0	1	0	4	3	1	2	1	1	1	0	1	1	0	0	1	0	2
184	0	0	0	1	0	0	0	1	2	0	2	0	0	0	1	0	0	0	0	0	0	1
185	1	1	2	4	0	2	2	4	5	1	2	1	1	1	2	2	1	1	1	1	1	2

APPENDIX 1. Continued

Site	Bla	Sym	Aca	Echinoph	Oxy	Euph	Parac	Poly	Heteroc	Cary	Bal	Rhiz	Den	Tub	Tur	Heterop	Tubip	Mille	Stylas	Unid	G	S
160	0	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	22	35
161	1	0	1	1	0	1	0	0	0	0	0	0	1	0	2	0	0	0	1	0	23	32
162	1	0	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	25	33
163	2	1	1	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	22	31
164	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	17	23
165	1	0	1	0	1	0	1	0	0	0	0	1	1	2	2	0	0	0	1	1	28	36
166	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	9	11
167	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	15	17
168	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	18	19
169	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	11
170	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	11
171	1	1	1	1	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	22	33
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	10
173	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	11	11
174	1	1	1	1	1	0	0	0	0	0	0	0	0	1	2	0	1	1	0	0	35	54
175	0	1	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	26	39
176	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	21
177	1	1	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	27	42
178	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	17
179	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	23	33
180	1	1	2	1	1	0	0	0	0	0	0	0	0	1	2	0	0	1	0	0	33	54
181	0	1	2	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	25	34
182	1	1	2	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	24	38
183	1	1	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	27	45
184	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	13
185	1	1	2	1	1	1	1	0	1	0	0	1	1	2	3	0	1	1	1	2	51	81

APPENDIX 2. DESCRIPTIONS OF CORAL COMMUNITIES IN OMAN

This appendix lists summary descriptions for 246 coral communities studied during the course of the coastal zone management project. It derives from a general environmental classification database. The grid coordinates on the National Survey Authority Map Series K6611 (1:100,000) are listed after the name of each site. A type A coral community is one with true framework development. A type B community is one where corals are settled directly on base rock, sometimes obscuring it almost entirely, but where there is no reef framework. A type C community has corals growing mixed with or bordered by dense seasonal phaeophyte (brown algae) communities. Where a coral list has been completed, the site number corresponding to Appendix 1 is listed after the community type classification.

Ra's al Jirri - Ra's Shaykh Mas'ud (DQ190015-220040)

Coral Community Type: A, B (site number 001)

Description: The coast is characterized by cliff of varying height falling to a base of tumbled rock boulders on sand at depths of 1-5m. Shallower rocks are encrusted by pale brown zoanthid (*Palythoa* sp.), with scattered corals deeper surrounded by algal turf. Some coves have abundant *P. damicornis*. There are numerous juvenile fishes, especially chaetodons, angelfishes, sergeant majors, and some *P. versicolor*.

Threats: gill net, ropes, lines, anchors, tarballs, litter ashore; fabric, litter in coral; use by Iranians results in direct damage to coral from anchors, ballast bags of sand dumped overboard, in addition to litter on shore and underwater.

Cove 1, Ra's Shaykh Mas'ud (DQ198022)

Coral Community Type: B (site number 002)

Threats: lines in coral.

Khawr Idah South (DQ200026)

Coral Community Type: A, B (site number 003)

Description: coral growth well developed south side where small patch of *Porites* fused into a solid flat-topped framework 1.3m thick. Elsewhere coral generally in dispersed patches formed of *Porites* with large tabular *Acropora*. Towards centre of bay large *Porites* (2-3m diameter to 4m maximum) fused to form substantial spurs. North side has small scattered corals on rock.

Threats: ropes, fabric in coral, tarballs.

Ra's Shaykh Mas'ud West (DQ214041)

Coral Community Type: B (site number 004)

Description: west side has good coral growth with 1-2m diameter *Porites* and large tabular *Acropora*. There is a dense (99% cover) patch of *P. damicornis*.

Threats: gill net in coral, tarballs, litter, flotsam; corals damaged by anchors and numerous sand-filled ballast bags of Iranian small boat traders.

Qabr Shaykh Mas'ud (DQ217042)**Coral Community Type:** B**Description:** attractive coral growth on rocks bordering and in middle of bay.**Threats:** tarballs, severe damage underwater caused by ballast bags, anchors, ropes, trash of Iranian small boat traders.***Ra's Salti Ali*** (DP237994)**Coral Community Type:** B (site number 005)**Description:** shallow sandy bay bordered by boulders, large undercut rock blocks, becoming larger toward point, scattered corals.**Threats:** severe damage by ropes, gill nets, anchor blocks; much smashed, dead coral, litter underwater, tarballs.***Ra's Shakhs*** (DP280997-284998)**Coral Community Type:** A, B (site number 006)**Description:** narrow, low reef parallel shore, maximum framework of rubble banks 0.5-1m, covered by *P. damicornis*, bushy and tabular *Acropora*; cover bushy/tabular *Acropora* 10-60% to 95% for *P. damicornis*; much coral on beach.**Threats:** gill nets, ropes, anchor blocks in and breaking coral; severe damage from monofilament net that had entangled coral, fishes and many lobsters and large crabs.***Khawr ash Shamm*** (DP340980)**Coral Community Type:** A, B (site number 007)**Description:** sheltered fjordlike bay; much shore fringed by coral; some well-developed *Porites* framework reefs; luxuriant *Acropora* thickets with fragile extended branches; patches *P. cactus* framework reefs e.g. DP324966; coral growth appears better developed central and inner bay than outer - many more patches framework reef and luxuriant *Acropora*.**Threats:** *Acropora* smashed by fish traps, anchors; coral hauled up in gill nets; gill nets, fish traps in coral; *Platygyra* white patch disease severe inner bay.***Khawr ash Shamm (Jazirat al Maqlab)*** (DP344974)**Coral Community Type:** A, B (site number 008)**Description:** almost entirely encircled by *Porites* framework reef with luxuriant thickets *Acropora* below, patches *P. cactus* and *P. ?decussata*; *Porites* reef best developed east side, 2-4m framework, solid.**Threats:** *Acropora* smashed by fish traps, anchors.***Khawr ash Shamm (Maksar)*** (DP395980)**Coral Community Type:** B (site number 009)**Description:** scattered coral 50-85% cover, predominantly *Platygyra*, *Cyphastrea*, *P. ?decussata*.**Threats:** cans underwater, *Platygyra* frequently have large white patches leading from yellow central patch of fine alga through white band to thin tissue bordering healthy area - no black band or other sign of infection; much dead coral.

Khawr ash Shamm (Jazirat Sibi) (DQ394004)**Coral Community Type:** A, B (site number 010)

Description: shallow sandy shelves east and west covered by coral; east side *Porites* leading to mix *Acropora* thicket, *Platygyra*, and *P. ?decussata* to slope with *P. ?decussata* reef framework >1m thick; west side mixed *Acropora*, scattered *P. ?decussata*, *Platygyra* to slope with *Acropora* and *P. ?decussata*; rest of island rocky steep slope with predominantly *Platygyra* in shallows and steep slopes, *P. ?decussata* other slopes.

Threats: much dead coral; *Platygyra* white patch disease.

Ghassah (DQ320026)**Coral Community Type:** A, B (site number 011)

Description: bay bordered by rock with scattered coral, patches tabular and bushy *Acropora*; talus banks scattered through bay with bushy *Acropora*; northeast corner DQ321035 fused flat-topped *Porites* reef, framework 0.5-1.5m thick, bordered by sand with scattered *Porites* <3m diameter and tabular *Acropora*.

Threats: much flotsam, old small tarballs, much dead coral.

Khawr Ghubb Ali (DQ350060)**Coral Community Type:** A, B (site number 012)

Description: bay fringed by narrow border coral, primarily bushy and tabular *Acropora*, *Porites*, *P. damicornis*, *Platygyra*, *P. cactus* - each predominant at different sites; talus banks, patches bushy *Acropora* extend well offshore in places of ca. 6m depth; massive corals hollowed out; southwest coves have fused *Porites* reefs with 1.5m framework, cover varies 70-99% at DQ324076; north side has several patches *P. cactus* with 1m framework; deep water corals (*Paracyathus*) collected off Ra's Shaykh.

Threats: anchor block, ropes, gill nets, fish trap, litter in coral; much dead coral.

Khawr Ghubb Ali (DQ324075)**Coral Community Type:** A, B (site number 013)

Description: shore fringed by reef fused *Porites*, framework 1.5m, cover 70-99%, bordered by rock with variety corals, predominantly *Platygyra* in shallows, bush and tabular *Acropora* deeper, or patches *P. damicornis*; all leafy, branching coral here and next site have extended branches.

Threats: anchor block, ropes, fish trap, litter in coral, much dead coral.

Khawr Ghubb Ali (DQ368060)**Coral Community Type:** A, B (site number 014)

Description: shore fringed by *Platygyra daedalea* in shallows leading onto bushy *Acropora*, with well-developed patch *P. cactus* reef, 1m framework.

Khawr Bustan (DQ360105)**Coral Community Type:** B

Description: bordered by patches *P. damicornis*, talus with bushy and tabular *Acropora*.

Jazirat Umm al Ghanam (DQ344126)**Coral Community Type:** B (site number 015)**Description:** gradual slope of tumbled rock to sand at 12m; between 2-10m rock 60-85% covered by coral, decreasing rapidly in extent to few corals scattered over sand at 12m; coral predominantly flattened *Porites*; *Stylophora* also common in flattened form.**Jazirat Umm al Ghanam (DQ356167)****Coral Community Type:** A, B (site number 016)**Description:** bay fringed north and south by *Porites* reef extending from flat-topped, fused framework (1.5-2m thick) in shallows to border 2-4m diameter *Porites* boulders; extends out of bay as scattered coral on rock.**Threats:** ropes in coral, litter, sack in coral.**Jazirat Umm al Ghanam (Ra's Salib) (DQ363170-366167)****Coral Community Type:** A, B (site number 017)**Description:** patches fused *Porites* - *P. damicornis*, scattered large *Porites* 2-3m diameter, *Montipora*, tabular *Acropora*; west side leading off shore dissected flat-topped fused *Porites* 1.5-2m framework.**Threats:** ropes, fish trap, gill net in coral.**Jazirat Umm al Ghanam (DQ361163-360152)****Coral Community Type:** A, B (site number 018)**Description:** shore fringed by continuous reef of fused *Porites*, <2m framework, or patches *P. damicornis*, whorled or branched *Montipora*, tiers tabular and bushy *Acropora*; scenic mix corals; cover 90-99% (live 80-95%).**Threats:** ropes, gill net, litter (cans, bottles, plywood, sheets aluminium, pipes, angle iron), raft in coral.**Jazirat Umm al Ghanam (DQ358132-352127)****Coral Community Type:** A, B (site number 019)**Description:** scattered large *Porites* (maximum 5m diameter) fused in patches with extensive banks *P. damicornis* and patches large tabular *Acropora*, very scenic in places, cover 80-95%, framework <1.5m; southeast headland bare current-scoured rock; east shore rock with dense coral 60-90% cover *Porites*, bushy and tabular *Acropora*, patches *P. damicornis*; narrow patches fused *Porites* in shallows, framework 1-1.5m; very large *Tubastrea* in <1m depth.**Threats:** ropes, anchor, litter (cans, drums, cardboard, fabric) in coral.**Khawr al Quway' (DQ374169)****Coral Community Type:** A, B (site number 020)**Description:** beach fringed by solid framework fused flat-topped *Porites* ca. 25cm thick in shallows, extends offshore reaching 1m thick and becoming dissected. At ca. 1.3m thickness framework breaks up into individual large *Porites* heads (1-2m diameter, 2.5m maximum) with spaces filled by tabular *Acropora* and *P. damicornis*; corals scattered down gentle slope to sand at 6m. Same pattern followed along entire east shore of strait,

i.e., intermittent small areas of *Porites* patch reef, patches of *P. damicornis*, scattered corals over rock-sand slope.

Threats: ropes, gill net, anchors in coral; tarballs.

Ra's Shuraytah - Al Makhbuq (DQ380190)

Coral Community Type: B

Description: rock boulders with scattered corals, strong currents.

Threats: 1 *A. planci* (westernmost sighting) seen feeding on tabular *Acropora*.

Khawr Fordha (DQ380170)

Coral Community Type: A, B

Description: shallow bay bordered by coral patches extending as banks offshore in ca. 8m; slope gradual, alternating talus with sandy patches, *P. damicornis* patches, and 80% cover bushy and tabular *Acropora* to sand 7-8m; coral best developed DQ386174 Ra's Rarak.

Threats: much litter, including ballast bags of Iranian small boat traders, much dead coral; many *A. planci* scars; 33 *A. planci* seen in group.

Ra's Rarak (DQ386174)

Coral Community Type: A, B (site number 021)

Description: fused flat-topped *Porites* reef off beach, 0.5-1m thick framework; north side massive fused castellated *Porites* to 3m diameter, 2m thick framework, some hollowed out; *Porites* <4m diameter maximum; very scenic.

Threats: fishing lines, ropes in coral, litter, tarballs ashore, many *A. planci* feeding scars; 1 large *A. planci* seen from surface, others tucked under coral.

Khawr Khayran (DQ390160)

Coral Community Type: A, B (site number 022)

Description: east side coral covered slope; predominantly bushy and tabular *Acropora*, mostly dead; shallows talus with small bushy *Acropora*. west side DQ389162-390166 slope covered <95% by bushy and tabular *Acropora* - talus - *P. damicornis* to 8-10m depth; also large patches whorled *Montipora* with framework 1-1.5m thick.

Threats: coral hauled up in nets, much litter (cans, bottles, linoleum, boxes, plastic bags); much dead coral; many *A. planci* feeding scars east and west; 33 *A. planci* seen from surface east side, 2 west, others tucked under coral.

Khawr Ran (DQ410164-414169)

Coral Community Type: B (site number 023)

Description: east shore fringed by coral; no framework development, but cover reaches ca. 70% predominantly tabular *Acropora* in upper 2-3m; below this coral assemblage variable and generally mixed, but poorly developed ending at 5-7m on sandy slope; toward south more dead, broken, tumbled coral; *P. damicornis* predominates in patches, and is an unusual field of 1-1.5m diameter "mushrooms" of isolated *Astreopora* colonies below *Acropora* zone at 3-6m. west shore bordered by similar coral with occasional large *Porites*.

Threats: much litter (cans, bags, bottles, cardboard, linoleum, Iranian trader's ballast sacks); considerable devastation by *A. planci*. 26 seen in concentrated patch (size <55cm).

Jazirat Abu Sir (DQ420182)**Coral Community Type:** A, B (site number 024)**Description:** northeast point narrow rock ledge to wall; ledge widens west with 30-40% cover scattered mixed corals; most cove has coral-covered slope, 80-99% cover, well-mixed patches *P. damicornis*, tabular *Acropora*, whorled *Montipora*, fused castellated *Porites* with 1m thick framework generally, but <3m one site, very scenic; south of cove (DQ420175) tumbled rock slope with patches scattered coral or 99% cover *Porites*.**Threats:** ropes, litter in coral; many *A. planci* feeding scars, much dead coral, 60 *A. planci* seen from surface.**Jazirat Abu Sir** (DQ418174)**Coral Community Type:** B (site number 025)**Description:** coral-covered slope, 80-99% cover *Porites* - tabular *Acropora* - *P. damicornis*, ends sand 12m.**Threats:** few *A. planci* feeding scars, 0 seen from surface.**Khawr Kumzar** (DQ420150)**Coral Community Type:** A, B**Description:** east side coral sparse, intermittent patches *P. damicornis* and 1 patch whorled *Montipora* off gravel beach DQ430146; west side coral better developed in 2 large coves DQ412145, 412155. See specific site descriptions for further details.**Threats:** gill net, fish trap, lines, linoleum in coral; coral dragged up by beach seine; *A. planci*.**Khawr Kumzar** (DQ417156-416148)**Coral Community Type:** A, B (site number 026)**Description:** southeast shore 4-5m deep shelf with 60% coral cover, predominantly tabular *Acropora*, 50:50 live:dead; further in bay slope covered <95% large patches whorled *Montipora* or *P. damicornis* separated by talus - tabular *Acropora* patches; inner bay north shore patches fused castellated *Porites* - exceptionally well-developed north: flat-topped in shallows with 1-1.5m thick framework, reaching 2-3m.**Threats:** gill net, fish trap, ropes, linoleum, freezer, much litter in coral; much dead coral; some *A. planci* feeding scars, 2 seen from surface, others tucked under coral.**Khawr Kumzar** (DQ412145)**Coral Community Type:** B**Description:** coral along south shore down gradual slope to 7m, predominantly tabular *Acropora* (only 1-5% alive, rest broken dead *in situ*) with patches *P. damicornis* ca. 70% dead; further north more live coral, especially tabular *Acropora* along edge coral band; north side similar, but narrower band coral.**Threats:** very little; much dead *Acropora*; numerous *A. planci* feeding scars, 22 seen from surface in 1 group.

"Salla" (DQ432147-440146)**Coral Community Type:** A, B (site number 027)

Description: east side outer bay rock with sandy shelves, scattered coral, 10-25% cover, west of gridline DQ440 slope gradual with coral patches <99% cover, much dead *Acropora* (*A. planci* predation), *P. damicornis*, bushy *Acropora*, castellated *Porites* patches (2m diameter heads, fused forming porous framework), much *Astreopora* 7m deep; *P. damicornis* patches inner bay; west side large patches fused castellated *Porites* 2.5-3m diameter, flat-topped in shallows forming micro-atolls (<5m diameter), framework <2m thick; large patch *P. damicornis*, whorled *Montipora*, abundant *Astreopora*.

Threats: gill net, fish trap, ropes damaging coral; much litter (cans, bottles, fabric, drum, ballast bag) killing coral; much dead coral; many *A. planci* feeding scars, 34 seen from surface east side (28 in group), 21 west side.

Khawr Ma'ili (DQ450130)**Coral Community Type:** A, B

Description: shores fringed by scattered coral growth; rock walls have encrusting species and less variety; tumbled rock boulders support denser and more varied coral assemblages, or patches of *P. damicornis*. See individual accounts for details.

Threats: severe: tarballs, flotsam, litter; main base for Iranian small boat traders who anchor on corals, litter beaches, seabed.

Khawr Ma'ili (DQ442146-440132)**Coral Community Type:** A, B

Description: coral covered rock slope; 20-60% cover live coral to 90% in *P. damicornis* patches; percent cover increases south of point; patch *Montipora* with framework ca. 1m thick, cover 80-90%; also patch 100% *Goniopora*.

Threats: extensive smashed overturned coral, talus patches; vast areas seen eaten by *A. planci*, feeding scars numerous, 34 seen from surface.

Khawr Ma'ili (DQ440131-439127)**Coral Community Type:** B (site number 028)

Description: west side cove rock shelf with <99% coral cover in healthy mixed assemblage in 1 patch bordered by talus slopes with predominantly *P. damicornis*; east side scattered coral heads and talus inner reaches with patches large *Astreopora* heads; here 30-70% cover and less consolidated than west side; south cove less coral, much rubble, *P. damicornis* over talus.

Threats: litter, sheets linoleum on coral; much dead coral; *A. planci* feeding scars, 4 seen from surface.

Jazirat al Khayl (DQ455165)**Coral Community Type:** A, B

Description: north coast has rock walls and shelves with scattered corals, patches of *P. damicornis*; northwest cove shallow sandy shelf with *Porites* heads, talus, patches *P. damicornis*; southeast DQ464163 6m shelf with scattered *Porites* reaching 30-40% cover maximum, and rock outcrops with scattered coral; 1 *Porites* head 5-6m diameter; south

coast has reef framework - see next record for details.

Threats: ropes in coral; much litter underwater; base for Iranian small boat traders causing severe litter problem; numerous *A. planci* scars, 30 large *A. planci* seen from surface in small area (<5 minute count).

Jazirat al Khayl South (DQ449165-462160)

Coral Community Type: A, B (site number 029)

Description: south coast generally fringed by well developed reef of *Porites* with extensive patches *P. damicornis* (especially in shallows, but occasionally down slope); *Porites* heads (<3-4m diameter) form scenic formations ending on silty rock slope at ca. 9m; cover <99%.

Threats: ropes in coral; much litter, tar ashore and underwater; Iranian small boat traders cause severe litter problem; many *A. planci* feeding scars, 7 large *A. planci* seen on top of coral.

Ghubbat al Khouse (DQ480130)

Coral Community Type: A, B (site number 030)

Description: areas of good coral with true framework development and cover <99%; deeper in bay coral growth thins out, typically sparse veneer ranging from 0-30% cover; talus banks common with localized outbreaks *A. planci* e.g. at DQ475118.

Threats: gill nets in coral; Iranian small boat traders cause severe littering of few small beaches and adjacent seabed, e.g. at DQ460115 very heavily littered with tins, bottles, other rubbish in sea, ashore, killing coral; large areas damaged coral; *A. planci*.

Ghubbat al Khouse (DQ462126-460115)

Coral Community Type: A, B (site number 031)

Description: slope coral covered; varies from mixed assemblage to patches covered by whorled *Montipora*, *Goniopora*, *P. damicornis*, *P. cactus*; corals sparser deeper in bay existing only as thin veneer; amount of broken, upturned corals, talus banks, litter increases further into bay; corals sparse in head of bay.

Threats: damage to corals possibly from anchors; Iranian small boat traders causing severe litter problem underwater, ashore.

Ghubbat al Khouse (DQ500118)

Coral Community Type: B (site number 032)

Description: typical inner bay environment: primarily bare rock with small scattered corals in shallows; shore large blocks rock undercut forming deep caves - oysters all dead inner parts, alive outer rocks.

Threats: litter on seabed.

Ghubbat al Khouse (islet) (DQ490137)

Coral Community Type: B (site number 033)

Description: mainland slopes gradually from shore to sand at 5-6m with occasional sheer drops, stepped ledges to 8-10m east of islet; slope covered by varied corals, including patches *Acropora*, *P. damicornis*, *Goniopora*, *Turbinaria*.

Threats: gill nets, fish trap, lines entangled and damaging coral; bags, bottles in coral.

***Ghubbat al Khouse* (DQ478145)**

Coral Community Type: A, B (site number 034)

Description: rock slopes from base of cliff to sand at 3-5m; slope covered <99% alternatively by tabular *Acropora* or *P. damicornis* with occasional large *Porites* heads.

Threats: numerous *A. planci* feeding scars; 14 large *A. planci* (diameter 42cm) seen from surface.

***Jazirat Bu Rashid (Tawakkul)* (DQ495204)**

Coral Community Type: B (site number 035)

Description: series of stepped ledges and walls to >40m; ledges covered by *Sinularia* and *Sarcophyton*; walls blanketed with small blue ?*Xenia*-type alcyonarian, scattered hard corals, purple gorgonian, yellow antipatharian, bright yellow-orange sponges, red colonial tunicates; many fishes.

***Northwest Point Musandam Peninsula* (DQ500154)**

Coral Community Type: A, B

Description: narrow coral reef <90% cover primarily *Porites* with tabular and bushy *Acropora*; rest of shore of this bight is rock with scattered coral and talus patches.

Threats: ca. 120 pairs trousers (Iranian trader's consignment) covering, killing coral; *A. planci* feeding scars.

***Ra's al Bab* (DQ503152)**

Coral Community Type: B

Description: bay fringed by generally bare scoured rock with scattered flattened coral colonies; head of bay has large *Porites* and *Platygyra* with variety of other small corals scattered on large rock boulders on sand in ca. 5-6m.

Threats: current eddies concentrate tarballs and other flotsam.

***Jazirat Musandam* (DQ525176)**

Coral Community Type: A, B (site number 036)

Description: scenic, well-developed reef of flat-topped fused and castellated *Porites* in north cove that runs south intermittently along entire west bight; *Porites* overlaid by patches *P. damicornis*, *Montipora* (with vertical branches in shallows, whorled down slope); zone of large *Porites* generally borders coral growth at 8-9m; reef has scenic mix corals with imposing castellated *Porites* separated by patches other corals.

Threats: litter in coral; abundant cans, bottles, fabric on seabed and in coral; Iranian small boat traders cause pollution problem; numerous *A. planci* feeding scars, 41 *A. planci* seen from surface.

***Jazirat Musandam* (DQ526184)**

Coral Community Type: B (site number 037)

Description: area of strong currents with scattered coral on rock; large tabular *Acropora*, patches 99% *Montipora* (branched) in shallows.

Threats: *A. planci* feeding scars, 2 seen from surface.

***Jazirat Musandam* (DQ535165)**

Coral Community Type: A, B (site number 038)

Description: bay fringed by well-developed reef of fused *Porites* (flat-topped in shallows, <4m diameter), and banks talus covered by *P. damicornis* or *Goniopora*, large patch *Echinopora*; west side especially well-developed with reef-flat of compacted talus; *Acropora* very rare, small colonies, eaten by *A. planci*; reef slopes to base generally of large *Porites* at ca. 10-12m on sand.

Threats: gill net, ropes in coral; tarballs; sand filled ballast bags, litter (plastic bags, cans, fabric) dumped by Iranian small boat traders smothering, killing, breaking coral; *A. planci* feeding scars.

***Jazirat Musandam* (DQ540162-530160)**

Coral Community Type: B

Description: rock boulders with generally few small scattered corals; substrate covered by coarse gravelly sand-shell fragments with fine cover alga; water turbid eddying.

Threats: 4 gill nets entangled in coral; numerous *A. planci* feeding scars, 34 seen from surface.

***Jazirat Musandam* (DQ517156)**

Coral Community Type: B (site number 039)

Description: large rock boulders covered by brown zoanthids, *Sinularia*, coral (20-50% cover among boulders, <80% on boulders).

***Ra's Qabr al Hindi* (DQ509154-516114)**

Coral Community Type: A, B

Description: from Ra's al Bab south the shore has steep-stepped ledges of largely barren rock with strong current scour; the cove DQ514113 has quieter shallower water with talus banks and *Porites* reefs covered by *Diadema*, *P. damicornis*, *Montipora*.

Threats: current eddies concentrate tarballs, flotsam; beaches heavily polluted by oil, litter; small beaches used by Iranian small boat traders causing heavy pollution; numerous *A. planci* scars.

***Ra's Qabr al Hindi* (DQ518116-523110)**

Coral Community Type: B

Description: tumbled rock with few scattered corals.

Threats: many *A. planci* feeding scars, 20 *A. planci* seen from surface.

***Dawhat ash Shisah* (DQ440060)**

Coral Community Type: A, B (site number 040)

Description: stony tidal flats with *Siderastrea*, *Acropora*, *Porites*, *Leptastrea*, *Goniopora*, *Favites* exposed low water springs; see individual site descriptions.

Threats: gill nets, lines, ropes in and dragged over coral; tarballs, flotsam, litter; *A. planci*.

Dawhat ash Shisah (Daw Sunni) (DQ499105)**Coral Community Type: B**

Description: coral covered slope, 80-99% cover, mixed assemblage; breaks up south toward headland and north toward beach; corals generally flattened colonies *Platygyra*, *Echinopora*, *Echinophyllia* typical of sheer or deeply shaded rock faces, but unusual abundance of large *Astreopora* colonies; patches *P. damicornis*.

Threats: some *A. planci* feeding scars.

Dawhat ash Shisah (Sharyah North) (DQ404080)**Coral Community Type: B (site number 041)**

Description: patchy coral on base of dead *Acropora* and numerous small massive coral species; cover 30-50% live and dead coral on sand ending at 5-6m in shallow sandy bay; shallow slope means coral extends further offshore than usual as a patchy thin veneer.

Threats: lines in coral; few *A. planci* scars in bay increasing to severe damage off north headland (90-95% *Acropora* eaten by *A. planci*), 15 large *A. planci* seen from surface with many more under coral.

Dawhat ash Shisah (Jazirat Sawda) (DQ453082)**Coral Community Type: B**

Description: west side slope covered >90% *P. damicornis* in large patch, few *Porites*, bushy *Acropora*; cliffs toward south end and centre beside cobble beach mixed assemblage *Porites* and sheets *Echinopora*, *Echinophyllia*. Not studied east side.

Threats: litter underwater; *A. planci*.

Dawhat ash Shisah (DQ410055)**Coral Community Type: B (site number 042)**

Description: sparse corals on rock increasing to *Porites* dominated assemblage towards north headland; 50-75% cover; *Porites* dominated deeper with *Platygyra* shallower and large patches *Echinopora*.

Threats: ropes, anchors in coral; few *A. planci* feeding scars.

Dawhat ash Shisah (DQ402050)**Coral Community Type: B**

Description: banks talus with small *Acropora*, *P. damicornis*; dead coral, talus abundant in shallows, more living coral scattered deeper; living coral cover increases toward headland from 25% maximum to 50% at point (of which 75% *Platygyra*). This pattern typical of shallow coves that characterise the west side of the bay, with few notable exceptions (e.g., *Porites* reef at DQ400066, coral assemblage at DQ404080 that described separately).

NOTE: visibility decreasing daily as plankton growth, bioluminescence, red tides increasing turning water khaki - aswad to locals who claim water in summer clear/abyadh; filamentous algal growth on rock proliferating.

Threats: *A. planci* feeding scars.

Dawhat ash Shisah (DQ411028)**Coral Community Type:** A, B (site number 043)**Description:** entire west shore fringed by well-developed reef of fused flat-topped *Porites* with solid 1-2+m framework.**Threats:** ropes in coral; *A. planci* feeding scars, several seen under coral.**Dawhat ash Shisah (Marboob) (DQ425016)****Coral Community Type:** B (site number 044)**Description:** west side dense patches *P. cactus*, large tabular *Acropora* giving way to coral encrusted rock (<80% cover) up to and around west headland.**Threats:** ropes entangled and dragged across coral; beach seine snagged some live coral; tarballs, flotsam ashore; much litter underwater; several *A. planci* scars, 3 *A. planci* seen from surface, others tucked under coral; beach used to careen boats, increasing litter pollution underwater, especially linoleum sheets.**Dawhat ash Shisah (DQ462018)****Coral Community Type:** B (site number 045)**Description:** rocks encrusted by corals; much dead *Acropora*; good nursery area for variety of fishes.**Threats:** flotsam, tarballs; numerous *A. planci* feeding scars clearly linked to dead *Acropora*; 3 *A. planci* seen exposed, many others tucked under coral.**Ra's Khaysah - Ra's Bashin (DQ494017-487968)****Coral Community Type:** A, B (site number 046)**Description:** this stretch coast fringed intermittently by coral assemblages of different kinds; DP486982-481986 has banks talus >1m thick covered 99% by tightly packed *P. damicornis*; next coves north have narrow fringe predominantly tabular *Acropora* on rock with many dead patches; see specific site descriptions.**Threats:** tarballs, flotsam on beaches; numerous *A. planci* feeding scars; *A. planci* cause of much dead *Acropora*.**Ra's Khaysah South (DQ476004)****Coral Community Type:** A, B (site number 047)**Description:** southeast point: slope of boulders with scattered corals; low cliffed headland between south cobble beach and north sandy beach has well developed *Porites* reef formed of <3-4m diameter fused *Porites* with >2m framework, compact, scenic castellated colony formations; few species this area, greater variety east over tumbled rock boulders.**Threats:** several *A. planci* feeding scars.**Ra's Khaysah South 1 (DQ481986-486981)****Coral Community Type:** B**Description:** rock boulders with 75% cover coral (of which ca. 80% tabular *Acropora*); much coral dead.**Threats:** numerous *A. planci* feeding scars, 2 seen from surface, others tucked under coral.

Ra's Bashin South (DQ485968)**Coral Community Type:** B (site number 048)**Description:** rock slope covered 80-90% by coral; tabular *Acropora* predominant to 3m; mixed assemblage below with predominance of massive corals. (Note: north side Ra's DP488968 patch of coral covered slope, <80% cover, mixed predominantly massive corals).**Threats:** ropes in coral; large devastated area coral, much dead *Acropora* (possibly *A. planci* related), numerous *A. planci* scars, many *A. planci* seen tucked under coral, 0 seen from surface.**Jazirat Umm al Fayyarin (DQ548956)****Coral Community Type:** B (site number 049)**Description:** island drops rapidly to great depth, but there are few narrow shelves where colonies *Porites*, *Platygyra*, *Symphyllia* established; elsewhere rock walls and steep slopes have scattered corals (<40% cover maximum); much yellow antipatharian and purple gorgonian; *Dendronephthya*; much *Tubastrea*, *Dendrophyllia* common.**Threats:** ropes and large gill net spread over reef; flotsam, grease in eddies around island; abundant *A. planci*, 63 seen from surface in 50m stretch east coast including 5 on 1 *Platygyra* colony, many others tucked under coral, some large *A. planci*, most small 18-24cm diameter.**Ghubbat Shabus (DQ460960)****Coral Community Type:** A, B (site number 050)**Description:** some well-developed coral communities in bay, generally in areas open to north or east; elsewhere corals occur as scattered colonies on rocky slopes (seldom >30% cover); north part of bay has very little coral; *Porites* clearly dominates as primary structural component where there is framework development; the double bays from DP437958-436951 are fringed by flat-topped *Porites* fused to form 1-1.5m thick solid framework, with few other corals; see specific site descriptions for details.**Threats:** gill nets, ropes in coral; litter underwater; *A. planci*.**Ghubbat Shabus (DP440957)****Coral Community Type:** B (site number 051)**Description:** rock slope with ledges covered 50-65% coral, 80% maximum; predominantly *Acropora* on flat shelf with walls covered by sheets different corals; well mixed diverse assemblage; no sign *A. planci*.**Ghubbat Shabus (DP455940)****Coral Community Type:** B**Description:** rock slope with sand and scattered corals, cover seldom >30%.**Threats:** trash on corals, including drum; *A. planci* feeding scars.**Ghubbat Shabus (DP460940-466938)****Coral Community Type:** A, B**Description:** east bay: coral better developed west side; *Porites* dominated but patchy; east

side steeper/sheer with scattered coral on rock; west bay: sheer east side 25-50% cover coral on rock; head bay shallow below stony tidal flat; outer west side patches reef development dominated by *Porites*.

Threats: gill net in coral.

Ghubbat Shabus (DP475925-480916)

Coral Community Type: A, B (site number 052)

Description: this double bay fringed by dense well-developed coral community; *Porites* dominant as scenic, castellated, multicoloured colonies; patches covered by *Goniopora* (entire slope), *P. damicornis*, *Acropora*, large sheets *Echinopora*; reef framework reaches 1.5m thick in places, best developed east bay and east side west bay; west side west bay coral continues as thin veneer over rock, breaking up towards headland into rock with patchy coral.

Threats: ropes, gill net, anchors in coral; anchor damage inner bay; litter in coral; several *A. planci* feeding scars, 1 *A. planci* seen from surface, many others tucked under coral.

Ra's Dillah North (DP486909)

Coral Community Type: B (site number 053)

Description: much sheer primarily bare rock around Ra's with scattered sheets of coral; small coves have shelves with some coral; 1 site snorkelled: 10-70% cover *Sinularia*, less cover live corals; highest cover over large rock blocks; scattered *Porites*, *Platygyra* over rock-sand shelf.

Threats: gill net in coral; wastage fishes (discarded dead fishes include sohal, angelfish, garfish); few *A. planci* feeding scars, 1 *A. planci* seen from surface.

Ra's Dillah South (DP488904)

Coral Community Type: B

Description: sheer wall off point, shelf in first small cove with huge boulders leading to slope of large tumbled boulders with caves down to >40m; scattered corals shallower to scattered purple gorgonian and yellow antipatharian deeper; 1 huge black coral (bushy grey).

Khawr Habalayn (DP400900)

Coral Community Type: A, B (site number 054)

Description: outer bay has steep/sheer rock walls with sheets encrusting corals, small shelves below wadis have limited coral growth; central bay prolific coral growth, dense patches *P. damicornis*, *Acropora*, fused *Porites* reefs; inner bay dense cover bushy *Acropora* in places, generally scattered coral with *Platygyra* predominant; DP945911 *P. damicornis* patches; DP437910 west side luxuriant tabular *Acropora*, east side cliffed, sheer; bays north of point at DP411925 lined by bushy *Acropora*, *P. damicornis* patches - also patches in centre shallow bays; Ghubbat al Ghazirah bordered predominantly *Platygyra* with *P. cactus*, small patches fused *Porites*, DP362953 80-99% cover predominantly *Platygyra* shallows, *P. cactus* slope and small patches bushy *Acropora* (*P. cactus* not as extended leaves as Khawr ash Shamm). See specific site descriptions for details.

Threats: gill net, fish trap, fishing lines, ropes in coral; litter ashore, underwater; much dead coral; severe coral damage from *A. planci*.

Khawr Habalayn (DP474906-473911)

Coral Community Type: A, B (site number 055)

Description: fused flat-topped *Porites* reef, framework 1-3m, *Porites* diameter 2-3m, banks *P. damicornis*, sheets *Echinopora*; very scenic, castellated, colourful *Porites*.

Threats: gill net, fishing lines, rope in coral; litter underwater; much dead *Acropora*; many *A. planci* feeding scars, 3 seen from surface, many tucked under coral.

Khawr Habalayn (DP425911)

Coral Community Type: A, B (site number 056)

Description: 10/04/86 beach fringed *Acropora* - *P. damicornis* west-centre, east *Montipora* with <1m thick framework; east headland tumbled rock slope with luxuriant tabular *Acropora*; further out cliffs extend underwater as rock walls with narrow ledges; sheer faces encrusted large sheets coral, 30cm *Tubastrea*. 13/01/90 *Acropora* areas off beach, headland wasteland of dead, broken coral, talus, some recolonisation outer bay and deeper edge; small *P. damicornis* patches off headland with *A. planci* scars; *P. damicornis* on dead *Acropora* off beach large dead patches (flood runoff or *A. planci*?).

Threats: litter underwater (cans, linoleum); *A. planci* predation: 10/04/86 27 seen from surface in 4,000 square metres, estimated 25% *Acropora* dead; 13/01/90 total devastation *Acropora*, *A. planci* still present, 3 seen from surface, others tucked under coral, feeding on *P. damicornis* off headland, *Montipora* off beach.

Khawr Habalayn (DP414950)

Coral Community Type: B (site number 057)

Description: slope, rock shelves covered 40-95% coral, predominantly bushy *Acropora*; large coral-encrusted blocks separated by narrow, sheer gullies; deeper shelves deeply undercut.

Threats: litter underwater; much dead *Acropora* and *A. planci* feeding scars; huge *A. planci* all tucked under coral.

Khawr Habalayn (Maksar) (DP395977)

Coral Community Type: B (site number 058)

Description: 1:1 sandy slope with ca. 40% coral cover, deeply undercut rock shelves with ca. 80% cover; predominantly *Platygyra* (no white patch disease like across ridge in Khawr ash Shamm).

Threats: some litter.

Khawr Habalayn (Jazirat Habalayn) (DP358938)

Coral Community Type: A, B (site number 059)

Description: island surrounded by coral, particularly well developed *Porites* reef northwest and north sides, 2-3m diameter colonies, 2-3m thick framework, patchy *Porites* reef elsewhere, large field bushy *Acropora* on wide shelf to south; cover 50-90% generally, 99% on *Porites* reefs and dense *Acropora* patches; west side assemblage

Porites-Stylophora-Platygyra -Acropora (bushy and large tabular).

Threats: ropes in coral; many *A. planci* feeding scars and devastated coral, 117 seen from surface in 15 minutes south side where devastation worst, many others tucked under coral; largest *A. planci* 57cms diameter. 28Apr90 recount *A. planci*: shallow *Acropora* on south shelf nearly all dead, fringes have living coral and numerous *A. planci* scars; most *A. planci* now deep or tucked under coral - not clustered as previously; 63 *A. planci* counted from surface in 25 minutes.

Khawr Habalayn (Habalayn) (DP327930)

Coral Community Type: A, B

Description: patches fused *Porites* off village; framework 1-1.5m thick DP330427.

Khawr Habalayn (Khawr Najd) (DP340903)

Coral Community Type: A, B (site number 060)

Description: coral reef similar appearance Khawr Shamm reefs dominated by large-blade *Pavona*, >1m thick framework; flat-topped, porous *Platygyra* in shallows.

Threats: anchor block in coral.

Khawr Habalayn (Nibah) (DP420850)

Coral Community Type: A, B (site number 061)

Description: fused flat-topped *Porites* reef with bushy and tabular *Acropora* from DP430853 intermittently into bay to islet DP415848; inner bay small patch *Acropora* as thin veneer DP412865; DP414866 sand-rock slope covered 80-90% by small bushy *Acropora*, some large dead tabular *Acropora*; scattered *Astreopora* on sand off seaward edge.

Threats: flotsam, bottles, broken glass, old tarballs ashore; 11/04/86 8 large *A. planci* seen from surface in 3000 square metres DP414866, possibly cause of dead *Acropora* tables, feeding scars seen from boat 13/01/90.

Khawr Habalayn (Nibah East) (DP430854)

Coral Community Type: A, B (site number 062)

Description: fused, flat-topped, porous *Porites* reef of 2-2.5m diameter colonies, 1.5-2m thick framework.

Threats: some obvious *A. planci* predation of bushy *Acropora*; no *A. planci* seen.

Khawr Habalayn (Yidiyah al Bahr) (DP438858-445860)

Coral Community Type: A, B

Description: flat-topped fused *Porites* reef ca. 300m long DP443856; patch bushy and tabular *Acropora* below cobble beach DP438854 with few *A. planci* scars; west shore *Platygyra-Acropora* (bushy, tabular) assemblage.

Threats: *A. planci* feeding scars.

Khawr Habalayn (DP455856-472855)

Coral Community Type: B

Description: steep to sheer rock walls with scattered sheets encrusting coral (majority this

section coast); shelves, rocky slopes denser coral assemblages; *Platygyra-Porites-Acropora* (bushy, large tabular) assemblages DP455856, 466854 cover 80-90%, and 472855 cover 65-80%.

Threats: *A. planci* feeding scars and 2 *A. planci* seen from boat each site.

***Ra's Sarkan - Ra's Secun* (DP477850-440808)**

Coral Community Type: B

Description: small coves have shelves 3-6m deep with rock boulders, few scattered corals (<5% cover usual, to 20-50% maximum in small discrete patches); shelves bordered by walls (<1% coral cover); *Dendronephthya*, *Tubastrea* from 2m down.

***Dawhat Qabal* (DP400800)**

Coral Community Type: A, B (site number 063)

Description: relatively shallow bay with rocky shore ending on sand at 3-6m; north coast has few scattered corals, small isolated patches *P. damicornis*; coral growth best along south coast where *Porites* fuse to form shore-fast, flat-topped reef framework 1-2m thick, exposed low water springs; framework reef at DP396784 (small), DP400787 (ca. 400m long), DP407783 (ca. 250m long), DP411781 (small), DP412782 (small), DP413783 (small), DP416782; also large patches *P. damicornis*, mixed coral assemblages (<60% cover in bay DP406785); small patch castellated *Porites* DP387798.

Threats: fish traps, gill nets, ropes, poles in coral.

***Dawhat Qabal* (DP415782)**

Coral Community Type: A, B (site number 064)

Description: sheer gullied rock each side wadi fan; rock boulder slope below fan covered by coral, predominantly *Porites* and *Platygyra* forming fused, flat-topped, porous 1.5m thick framework; *Porites* 1.5-2m diameter; large patch *H. exesa* down slope.

***Ra's Marovi* (DP430743)**

Coral Community Type: B (site number 065)

Description: an apron of sand slopes north and south from the narrow tidal bar joining the west island to the mainland; north slope covered by rock, mixed corals, *Sinularia*; south slope has patches *P. damicornis* bordered by walls with fringe tumbled rock, coral cover 25-75%; north island sheer wall with large colony purple gorgonians, large *Tubastrea*, much *Dendronephthya*; *Dendronephthya* abundant all around island in orange, mauve colours; *Sinularia* also abundant and predominant on south side shelves; southeast shelf large with scenic, colourful mix corals; parts south sheer, deeply undercut walls.

Threats: gill nets, ropes in coral; corals and small lobsters in tangle net; few cans, bottles on seabed; many *A. planci* feeding scars, 1 seen exposed, others tucked under coral.

***Ma'awi* (DP404731)**

Coral Community Type: A, B (site number 066)

Description: large patch tiered *Acropora* (1-1.5m thick framework, 2-3m diameter tables, 100% cover with sand patches, 95% live, extends from shore to fringe *Sinularia*, sand 4m depth; other corals confined to edges, sandy patches. Similar smaller table *Acropora* patch

DP410741.

Limah (DP425700)

Coral Community Type: B (site number 067)

Description: north end beach DP425708 small patch coral *Porites* (<2.5m diameter), *P. damicornis*, tabular *Acropora* predominant.

Threats: anchor block, lines, ropes, gill net, fabric, plastic bags, cans in coral; large patch of long-dead big tabular *Acropora*; some *A. planci* scars, 0 seen from surface - all tucked under coral.

Jazirat Limah (DP468695)

Coral Community Type: B

Description: walls to >30m cut by fissures, overhangs and caves; shelves with large rock boulders forming arches, tunnels; scattered hard corals, abundant purple gorgonians and yellow antipatharian, *Sinularia* and *Sarcophyton*; many fishes.

Threats: ropes, gill net in coral.

Ra's Limah South (DP440687)

Coral Community Type: B

Description: extensive patches *P. damicornis* fill cove, inner side large heads *Porites*, rock with scattered corals.

Threats: gill net in coral.

Ghubbat Aqabah (DP400670)

Coral Community Type: A, B (site number 068)

Description: shallow bay with tumbled rock or low cliffed shore to sand; wherever shallow rock shelves (i.e. below wadis, in coves) may be some *Porites* reef development or dense cover by bushy and tabular *Acropora* which now dead and secondarily colonized by other corals (especially *P. damicornis*); extensive dead coral, talus banks.

Threats: severe: lines, ropes, gill nets, fish traps, cans, fabric, bottles, drums, plastic bags and sheets in coral; extensive dead coral; *A. planci*.

Ghubbat Aqabah (Ra's Samut) (DP437677-424680)

Coral Community Type: B (site number 069)

Description: talus banks on shelves, much dead bushy, tabular *Acropora* on rock and down slope to sand 4m; coral on rock walls and boulders below healthy (cover 3-50%); small cove (DP434681) has slope carpeted by *Goniopora* (ca. 80% cover).

Threats: severe: 4 gill nets, ropes, lines, poles entangled and damaging coral; 4 drums, cans, bottles, plastic in coral; many *A. planci* feeding scars, all *A. planci* tucked under; much dead *Acropora*.

Ghubbat Aqabah (Aqabat) (DP416676)

Coral Community Type: A, B

Description: small solid patch fused *Porites* reef leading from flat-topped reef-flat (0.5-1m thick framework) down short slope (1.5m maximum framework) to large knobbed *Porites*

heads on sand in 3m; *Porites* <2m diameter hollowed in places; dense small *P. damicornis* banks seaward.

Threats: gill net, ropes in coral; much dead bushy and tabular *Acropora*.

Ghubbat Aqabah (Al Haqil) (DP394686)

Coral Community Type: B

Description: shallow sand with rocky patches, extensive area of diffuse large tabular *Acropora* and *Porites* colonies, no cohesive reef structure; ca. 50% cover.

Ghubbat Aqabah (DP395649)

Coral Community Type: A, B (site number 070)

Description: *Porites* fused to form flat-topped tidal platform, ends sand 1-1.5m, highly porous hollowed out and solid framework.

Threats: lines, fish trap in coral.

Sidwen (DP400628)

Coral Community Type: B

Description: south shore fringed by band *Porites*, *P. damicornis* patches, tabular and bushy *Acropora*; 30-75% cover.

Massar (DP375604)

Coral Community Type: B (site number 071)

Description: tiers of tabular *Acropora* on rock, 2-2.5m diameter >80% cover.

Threats: rope in coral; many *A. planci* feeding scars; 1 *A. planci* seen from surface, others tucked under coral; patches broken tabular *Acropora*.

East Coast Musandam (DP382589)

Coral Community Type: A, B (site number 072)

Description: fused, flat-topped *Porites* (<3m diameter) reef, 1-1.5m thick framework; outer bay scattered *Porites* and *P. damicornis* patches; dense banks *P. damicornis* north side; beautiful coral garden south side.

Threats: ropes, gill net, fish trap, anchor in coral.

Dawhat Sharyah (DP370575)

Coral Community Type: A, B

Description: DP370578 shallow shelf with large patch bushy and tabular *Acropora*; DP365573 shallow fused, flat-topped *Porites* reef, 1-1.5m thick framework.

East Coast Musandam (DP369563)

Coral Community Type: A, B (site number 073)

Description: fused, flat-topped *Porites* (3-3.5m diameter) reef, 1-1.5m thick framework; continues offshore as tiers tabular *Acropora* (2m diameter) and rock covered 80% by corals.

Threats: gill net in coral; numerous *A. planci* feeding scars and dead tabular *Acropora* southeast side cove; 1 *A. planci* seen from surface, others tucked under coral. *Porites* in

shallows pitted by *Echinometra*.

Sanat (DP357543)

Coral Community Type: A, B (site number 074)

Description: east shore has banks of *P. damicornis*, and bushy and tabular *Acropora*; west shore has extensive fused *Porites* reef fringing almost entire length with bushy and tabular *Acropora*, *P. damicornis* along reef edge; 1-3m thick framework, 2-4m diameter *Porites*.

Threats: gill net, fish trap, ropes in coral; litter underwater, tarballs; much dead tabular *Acropora*; shallow *Porites* pitted by *Echinometra*.

Khawr Mala (DP345530)

Coral Community Type: B

Description: shore fringed by bush and tabular *Acropora*, especially outer half east shore.

Dawhat Haffah (DP310480)

Coral Community Type: A, B (site number 075)

Description: DP298474 very solid narrow finger *Porites* reef, 0.5-1.5m thick framework; much sponge; DP298474 and 311475 narrow *Porites* reefs.

Threats: gill net, fish trap, ropes, anchor blocks, fabric, plastic bags, cans in coral.

Zaghi (DP272435)

Coral Community Type: B (site number 076)

Description: south headland has rocky shore with rock slope and large rock blocks underwater; parts covered by dense coral, predominantly tabular *Acropora*, *Porites*.

Threats: severe damage by gill nets, ropes; litter/flotsam on beach and underwater; many tarballs.

Zaghi South (DP276416)

Coral Community Type: B (site number 077)

Description: south side beautiful coral garden; tiers tabular *Acropora* (<2.5m diameter), 95% cover.

Threats: gill net, ropes in coral.

Ra's Sawt North (DP279410)

Coral Community Type: B (site number 078)

Description: north facing shore from cobble beach to point is fringed by tiers of tabular *Acropora*, densest below beach, sparser toward point.

Threats: 2 large gill nets flat over coral (now dead/damaged); many ropes in coral.

Daba North (DP272400)

Coral Community Type: B (site number 079)

Description: north end beach bordered rock shore with scattered corals on rock boulders in shallows; further offshore and around headland 50-65% cover coral, predominantly tabular *Acropora* (1.5-2m diam) mixed with *P. daedalea* and *Porites*.

Threats: numerous gill nets, ropes and fishing lines, fish traps in coral.

Ra's Sawadi* (EM790295-814280)*Coral Community Type:** A, B (site number 080)**Description:** assemblages of coral colonies on rock occur around the smaller islands, off the north and west sides of Maqbarah, and along the north coast of Jabal 'Add, forming a few small patches of coral framework <1m thick; finest coral (highest percentage living cover, least damage, most extensive area), *Stylophora-P. damicornis-Acropora* (tabular and bushy) assemblage off western island, but heavily infested with *A. planci* (13 counted from surface in 2 minutes).**Threats:** considerable coral breakage in shallows around central islands caused by recreational boaters.***Daymaniyat Islands (General)* (EM967380-FM200370)****Coral Community Type:** A, B (site number 081)**Description:** many well-developed framework reefs (generally 1-3m thick, but reaching 4m) formed of *Porites* and *P. damicornis*; typically north shores have cliffs falling to tumbled rocky slopes between 6 and 25m deep with abundant coral growth; southern shores shallow, often with banks of *P. damicornis* forming ribbons of reef parallel to shore at depth of 6-8m; clearly area of former luxuriant coral growth, but many large *Acropora*, *Porites*, *Symphyllia* colonies now dead; amount of dead coral (cover up to 99%) is a remarkable feature of many of the reefs; one patch *Galaxea* south of Jun forms framework reef 40x10m and 1m thick - unique in Oman.**Threats:** ropes, fishing lines, gill nets in corals causing considerable damage; collection *Lambis truncata* and *Pinctada* by fishermen for sale to people on mainland; *A. planci*; collection shells and lobsters and spearfishing by expatriates.***Daymaniyat Islands (Clive Rock)* (EM967380)****Coral Community Type:** A, B (site number 082)**Description:** large, predominantly sand-covered shoal with largely dead vestiges of former framework reefs scattered over it and around the rim; shoal slopes from ca. 8m down talus-strewn slopes except in northeast where rock rim drops sheer to sand at 20m; rim of north slope has largely dead and dissolving framework reef with numerous small heads of *Porites* (not clear whether these are vestiges of former colonies or new growth).**Threats:** gill net in corals.***Daymaniyat Islands (West Jun)* (EM987366)****Coral Community Type:** A, B (site number 083)**Description:** large rock outcrop with slopes to 15-20m and sheer drop to 23m; few scattered corals; southwest slope rock-sand 60% coral 40%, much dead tabular *Acropora* (formerly huge colonies >3m diameter), *Porites* framework reef 75% dead.***Daymaniyat Islands (East Jun)* (FM000364)****Coral Community Type:** A, B (site number 084)**Description:** Well-developed reef of large fused *Porites* with 3-4m thick framework fringes southeast shore; several large banks 99% live *P. damicornis* 2-3m thick south of cut between this and next island east.

Threats: gill nets, ropes in coral, one net laying flat over vast area, another rolled up with coral bouncing over reef causing extensive damage; spearfishing, lobster catching by Naval personnel.

Daymaniyat Islands (Island east of Jun) (FM001364)

Coral Community Type: A, B (site number 085)

Description: *Porites* framework reef (2m thick) southwest side island, narrows east, breaks up onto talus slope with large dead tabular *Acropora*; remarkably few other corals on reef; low banks *P. damicornis* offshore.

Threats: *A. planci*, 3 seen exposed eating *Porites*.

Daymaniyat Islands (western central island) (FM076384-093387)

Coral Community Type: A, B (site number 086)

Description: shallow south side with numerous patches and scattered heads of coral, some small framework reefs (<1m thick) formed of *P. damicornis*, *Acropora*, *Montipora*, banks of *P. damicornis* further offshore; north side deeper with abundant coral along tumbled rock base of cliffs, framework reefs in east bay.

Threats: extensive damage to corals from gill nets.

Daymaniyat Islands (west, western central island) (FM076384)

Coral Community Type: B (site number 087)

Description: sheer rock drop to 20m from rock ridge (6m); generally small corals, numerous bases large, long-dead, tabular *Acropora*; vertical faces encrusted *Tubastrea* and variety sessile invertebrates.

Threats: gill net in coral, large gastropods entangled.

Daymaniyat Islands (northwest, western central island) (FM077384)

Coral Community Type: B (site number 088)

Description: vertical wall to tumbled rock from 6-15m; abundant corals; vertical walls encrusted *Tubastrea*; large patch *Goniopora* (99% cover); shallower surfaces (3-8m depth) large rock blocks covered >95% by encrusting *Montipora*, *Porites*, *Platygyra*, *Acropora* (bushy); much long-dead, tabular *Acropora*.

Daymaniyat Islands (east point, western central island) (FM090387)

Coral Community Type: B (site number 089)

Description: east point has rock ledge with abundant bases of large, long-dead, tabular *Acropora* dropping vertical to sand at 14m.

Threats: gill net caught in corals along wall with entangled remains of hawksbill turtle.

Daymaniyat Islands (northeast bay, western central island) (FM090385)

Coral Community Type: A, B (site number 090)

Description: northeast bay filled with flat-topped fused *Porites* reef (framework 1-1.5m thick), forms mosaic over sand (coral 80%:20% sand).

Daymaniyat Islands (island west of main island) (FM103386-112390)**Coral Community Type:** A, B (site number 091)**Description:** framework reefs of *Porites* northeast and *P. damicornis* southeast; remarkable amount of dead coral.**Threats:** ropes, gill nets, fish traps entangled in and killing coral.**Daymaniyat Islands (north, island west of main island) (FM106390)****Coral Community Type:** A, B (site number 092)**Description:** rock with extensive dead coral, including abundant bases of long-dead, tabular *Acropora*, *Porites*, *Symphyllia*; east side this bay corals abundant, *Porites* forms reef framework >3m thick.**Threats:** net in corals.**Daymaniyat Islands (south, island west of main island) (FM111386)****Coral Community Type:** A, B (site number 093)**Description:** series of banks parallel to shore of living *P. damicornis* with few other corals; shore-fast rock reef with scattered corals leading west to extensive area large dead tabular *Acropora*, *Porites*.**Threats:** gill nets, fish traps entangled in and killing coral.**Daymaniyat Islands (main island) (FM116393-131391)****Coral Community Type:** A, B (site number 094)**Description:** rocky coast of island supports abundant coral growth, but much currently dead; several small framework reefs of *Porites*, with best example in bay southeast of guard house.**Threats:** *A. planci*; ropes, nets in coral; collection shells (*Lambis truncata* and *Pinctada*) by fishermen for sale to people on mainland.**Daymaniyat Islands (southwest, main island) (FM118388)****Coral Community Type:** A, B (site number 095)**Description:** large talus patches with small scattered coral colonies, much dead coral in shallows (particularly tabular *Acropora*); patches and low banks *P. damicornis* at 5m depth and out.**Daymaniyat Islands (northwest, main island) (FM116394)****Coral Community Type:** B (site number 096)**Description:** rock outcrops and ledges with coral cover varying from scattered (<10%) to dense (>60%) in small patches, drops sheer to sand at 15m.**Threats:** *A. planci*, one seen exposed; ropes, nets in coral.**Daymaniyat Islands (rock patches south main island) (FM126387)****Coral Community Type:** B (site number 097)**Description:** rock outcrop (5m deep top to 10m sand) festooned with long-dead bases of large, tabular *Acropora*, many small coral colonies; north slope carpeted by *P. damicornis*.**Threats:** *A. planci*, one seen exposed

Daymaniyat Islands (south, main island) (FM128389)**Coral Community Type:** A, B**Description:** large well-developed framework reef (4-5m thick) of huge *Porites*; rock shelf in shallows covered >75% bushy *Acropora* with large dead tabular forms; banks *P. damicornis* (>2m thick) around seaward edge.**Daymaniyat Islands (southeast, island east main island) (FM134393)****Coral Community Type:** A, B**Description:** shallow basin rimmed by rock, washed by strong current; scattered corals on rock with long-dead bases huge tabular *Acropora*, fused *Porites* reef (framework ca. 4m thick) borders south rim, large patch *Psammocora* west.**Daymaniyat Islands (west, east island main group) (FM134394-143395)****Coral Community Type:** A, B (site number 098)**Description:** current-scoured smooth rock surface largely devoid of corals west side channel; patch *Porites* framework reef (>2m thick) on west side; abundant corals along south rocky reef between surface and 15m.**Threats:** *A. planci*, 1 seen exposed.**Daymaniyat Islands (east, east island main group) (FM143395)****Coral Community Type:** B (site number 099)**Description:** steep drop over narrow ledges to sand 22-27m depth; corals more abundant south of east point than north side, but these small and relatively low cover; rock densely covered by sponges, tunicates, purple gorgonians, yellow antipatharians, *Dendronephthya*.**Threats:** *A. planci*, 17 seen exposed, 1 feeding on *Dendronephthya*; net fish trap in coral.**Daymaniyat Islands (New Reef) (FM150360)****Coral Community Type:** A, B (site number 100)**Description:** large rock-sand shoal with rock outcrop from 4-5m deep to >25m; south and west sides sheer, north and east sandy platform with coral patches, *Porites* reef framework (1-1.25m thick), abundant living coral.**Threats:** nets, fish trap in coral.**Daymaniyat Islands (Kharabah) (FM190367-200370)****Coral Community Type:** A, B (site number 101)**Description:** south: series of banks (2-4m thick) of >85% living *P. damicornis* 200-300m offshore, 8-11m deep, alternating with rock covered by dead tabular *Acropora*, and talus slopes; east side: rock-sand shelf with scattered solitary *Porites* heads (1-1.5m diameter) and large patch *P. damicornis* leading onto a well-developed but small framework reef of fused *Porites* (ca. 2m thick) along west side emergent rocks; extensive rock platform east with scattered corals (predominantly exhibiting encrusting or small robust growth forms); alcyonarians (*Sarcophyton*, *Sinularia*) carpet the rocky ridges and eastern rim of this reef which drops sheer over a number of ledges to sand at 24m; north side: coral best developed along the north slope of the reef (see next account); northwest and west sides: considerable dead coral here including large colonies of *Symphyllia*, *Acropora* (tables).

Threats: *A. planci*, ropes, nets in coral.

Daymaniyat Islands (Kharabah) (FM194371)

Coral Community Type: A, B (site number 102)

Description: gentle slope away from island with shelf at 13m depth with many scattered corals; at 8-10m depth is large area *Porites* reef extending east-west and forming >1m thick framework; below this is a band of >75% dead coral.

Threats: net in corals; *A. planci*, 6 seen exposed in short stretch.

Fahal Island (FM530195)

Coral Community Type: A, B (site number 103)

Description: island surrounded by diverse coral communities, including incipient *P. damicornis* patch reefs (2-3m thick framework), and mixed assemblages of smaller coral colonies on rock; abundant deep water corals on rock outcrops.

Threats: gill nets, ropes, fish traps, fishing lines, litter, boat anchors in and damaging coral; coral and shell collection; heaviest diving activity in Oman; *A. planci*.

Fahal Island Southeast (FM530194)

Coral Community Type: A, B (site number 104)

Description: *P. damicornis* reef in 6-8m (2-3m thick framework) sloping to border *Porites* boulders; rock shelf at 12m, dead coral and patchy small colonies living corals.

Threats: boat anchors, ropes, gill nets, fish traps in coral; conspicuous *A. planci* feeding scars on *P. damicornis*, 3 exposed, others tucked under coral.

Fahal Island West (FM529195)

Coral Community Type: B (site number 105)

Description: rock shelf with gentle slope (6m deep) covered by abundant small corals (flattened, encrusting); at 10m drops vertically to sand at 18m.

Threats: anchors, ropes, nets in coral; *A. planci*.

Fahal Island (Shallow Reef) (FM536199)

Coral Community Type: B (site number 106)

Description: two large rock outcrops encrusted with sponges, molluscs, corals, alcyonarians.

Threats: heavily dived - located by dragging anchors; gill net draped over.

Fahal Island (Deep Reef) (FM536199)

Coral Community Type: B (site number 107)

Description: large, deep (22-42m) rock outcrop covered by deep water corals and alcyonarians.

Threats: divers locate by dragging anchors.

Ra's al Hamra North (FM527162)

Coral Community Type: B (site number 108)

Description: low rocky ridges 13-15.5m deep with numerous sponges, gorgonians,

crinoids, zoanthids, alcyonarians, and corals; *Siderastrea*, *Anomastrea* large and common; sole location *Acanthastrea maxima* with >8cm diameter calyces.

Threats: gill nets set in vicinity, overturn corals.

Darsayt (FM580148)

Coral Community Type: A, B (site number 109)

Description: Rock outcrop with mixed corals from 3-4m to sand at 14m, surrounded by fringe huge *Turbinaria*; *P. damicornis* forms banks with 1-2m thick framework southeast and in bay.

Threats: gill nets; *A. planci*.

Aint East (FM588146)

Coral Community Type: B (site number 110)

Description: generally steep rock to cliff extending as tumbled rock underwater with corals reaching 85% cover in places

Threats: nets on reef; collection of corals.

Kalbuh (FM617136)

Coral Community Type: A, B (site number 111)

Description: rock with corals from shore across bank dead *P. damicornis* to border large *Porites* boulders (<3-3.5m diameter, some fused to form framework) alternating with mixed *Porites-P. damicornis* and *Porites-Platygyra*, drops abruptly to sand at 5m with patches *P. damicornis*; extremely scenic coral garden with *Acropora* (bushy and tabular) predominant.

Threats: heavily used by divers, especially for training, some breakage; ropes, fishing lines, gill net, abundant litter in coral.

Muscat Island (East Coast) (FM632137-634132)

Coral Community Type: A, B (site numbers 112, 113)

Description: rocky coast with well-developed coral communities in coves northeast, southeast and along south shore; massive corals fused to form small patches framework reef; *P. damicornis* forms banks along south shore with 2-3m thick framework.

Threats: ropes, gill net in corals.

Cemetery Bay (North Bay) (FM633122)

Coral Community Type: A, B (site number 114)

Description: dense coral cover (*Acropora*, *Porites*) flanks shores, better developed north shore; small bank largely dead *P. damicornis* toward mouth bay with 1-1.5m thick framework.

Threats: much dead coral.

Cemetery Bay (East Cove) (FM635119)

Coral Community Type: A (site number 115)

Description: small reef formed of huge fused *Porites* (3-5.2m diameter) with reef-flat secondarily colonized by other corals; 3m thick framework.

Cemetery Bay (Pillar Rock) (FM637121)**Coral Community Type:** B (site number 116)**Description:** rock walls and boulders encrusted by sheets *Leptastrea* and variety small corals from surface to sand at 21m.**Cemetery Bay (Headland South) (FM638117)****Coral Community Type:** B (site number 117)**Description:** cliffs to underwater terrace dropping sheer to sand at 18-20m covered by scattered coral colonies.**Cat Island (FM642092)****Coral Community Type:** A, B (site number 118)**Description:** islet slopes over tumbled rock with scattered corals to 13m on seaward side; rock shelf with dense cover of alcyonarians and corals, fused *Porites* and banks *P. damicornis* border rest of islet; *P. damicornis* bank southeast forms 1-1.5m thick framework and extends to sand at 8m.**Threats:** gill net and ropes in coral; heavily dived.**Al Bustan (FM653075)****Coral Community Type:** B (site number 119)**Description:** predominantly rock with scattered corals and patches *Sarcophyton*.**Threats:** nets, ropes, litter entangled in coral; much dead/broken coral.**Qantab (FM668068)****Coral Community Type:** B (site number 120)**Description:** tumbled rock below cliff to 6-9m, covered by dense coral cover (25-85%) including large *Symphyllia* colonies.**Threats:** many gill nets, ropes entangled in and killing coral; *A. planci* (2 seen exposed, others tucked under coral); >50% corals dead or damaged.**Bandar Jissah (General) (FM685060)****Coral Community Type:** A, B (site number 121)**Description:** mainly rock boulders covered by scattered corals, with small patches framework reefs (ca. 1m thick) formed of *Porites*, *Cyphastrea*, *P. damicornis*.**Threats:** numerous ropes, nets, fishing lines in coral; *A. planci*.**Bandar Jissah (FM676064)****Coral Community Type:** B (site number 122)**Description:** gentle rock slope from undercut rock shore to sand at 8-9m covered by algal turf, alcyonarians (*Sarcophyton*, *Sinularia*) and scattered corals; towards point cover alcyonarians and corals increases to 95-99%.**Bandar Jissah (Central Islet Southwest) (FM682056)****Coral Community Type:** A (site number 123)**Description:** narrow reef *Porites* with 1.5m thick framework.

Threats: knobbed smashed *Porites*, pieces removed.

Bandar Jissah (Central Islet North) (FM684057)

Coral Community Type: B (site number 124)

Description: steep rock slope to sand at 12m with numerous small encrusting coral colonies, tabular *Acropora*, large *Turbinaria*.

Threats: very disturbed area, many corals broken or overturned; many ropes, nets in corals; *A. planci* (5 seen exposed).

Bandar Jissah (East Cove) (FM686053)

Coral Community Type: A, B (site number 125)

Description: banks *P. damicornis* along shore (framework 1-1.5m thick); offshore small unusual reef dominated by *Cyphastrea serailia*, *Hydnophora exesa*, *Platygyra daedalea* (framework ca. 1m thick); low numbers small colonies other corals.

Bandar Jissah (FM687050)

Coral Community Type: A, B (site number 126)

Description: rock platform covered by alcyonarians and scattered small coral colonies; corals larger toward point forming a narrow framework reef dominated by fused colonies of *Platygyra* in the north and *Porites* in the south.

Threats: *A. planci* (1 seen exposed).

Khawr Yenkit (FM741037)

Coral Community Type: A, B

Description: east and west shores near mouth bordered by reef of fused *Porites* (framework 2m thick), porous due to bio-erosion, more extensive east side.

Threats: *A. planci*, 2 seen exposed; gill nets, ropes in reef.

Bandar Khayran (General) (FM770025)

Coral Community Type: A, B (site number 127)

Description: best coral development in Muscat area; abundant coral on rock slopes, boulders and walls; best developed framework reefs dominated by *Porites*, tiered *Acropora* reefs; almost entire shoreline of bays (excluding innermost one) fringed by rocky shores with abundant coral reaching >75% cover in many locations; numerous patch reefs.

Threats: heavy diving activity; intense fisheries, many entangled gill nets, ropes, fishing lines, litter breaking/killing coral.

Bandar Khayran Northwest (FM 757029)

Coral Community Type: A (site number 128)

Description: reef framework of fused *Porites*

Threats: poor condition, much dead or damaged coral and rubble along base of reef (10m); gill nets and ropes in reef.

Bandar Khayran (Main Bay South Shore West) (FM758022)**Coral Community Type:** A (site number 129)**Description:** only such reef in Muscat area: dominated by *Acropora* spp. (bushy and tabular) forming framework >1m thick; large (2m diameter), whorled table corals in tiers down slope bordered by bushy forms at 10m.**Threats:** some smashed corals in shallows; many ropes in coral.***Bandar Khayran (Main Bay South Shore East) (FM760022)*****Coral Community Type:** A (site number 130)**Description:** 2-3m thick framework of fused *Porites* with small colonies of other corals, leading from contiguous *Acropora* reef FM758022.**Threats:** gill net and ropes in coral.***Bandar Khayran (Islet) (FM762023)*****Coral Community Type:** A, B (site number 131)**Description:** rock covered 55-95% by a generally mixed assemblages of colourful corals drops to sand at 8-9m; patches may have clear predominance of e.g., *Acropora*, *Acropora-Stylophora*, *Porites*, *P. damicornis*, or *Pavona cactus*; fused *Porites* reef extends west for >100m with framework thickness increasing from 0.5 to >3m below which reef slopes to sand at 12m; this best developed true framework coral reef in Muscat area.**Threats:** ropes, nets in reef; corals broken by divers and fishermen; overturned *Acropora* tables.***Bandar Khayran (East Island North) (FM783026)*****Coral Community Type:** B (site number 132)**Description:** north cove bordered by rock with algae and alcyonarians predominant; scattered corals; some large *Goniopora* on west side of cove.**Threats:** anchors of diving boats.***Bandar Khayran (East Island Northeast) (FM784024)*****Coral Community Type:** A, B (site number 133)**Description:** north of small beach is patch of delicately branched *Montipora* which leads north to a patch of dead coral followed by a small bank of *P. damicornis*; beyond this is a beautiful example of a fused *Porites* framework reef (>2m thick) dropping to sand at 6-8m; north of this reef are steep rock slopes and walls with scattered corals.**Threats:** *A. planci*, 1 seen exposed; gill net in reef.***Bandar Khayran (East Branch) (FM784021)*****Coral Community Type:** A (site number 134)**Description:** reef fringes much of rocky shore of this eastern branch of the Khayran bays complex; in centre is well formed *Montipora* patch reef surrounded at 4-5m depth by a fringe of *Acropora* (east to south), *Astreopora* (southwest), *Hydnophora* (west-centre) and *Platygyra*; abundant *Diadema*.**Threats:** gill net in corals; much dead coral.

Ra's Khayran (Sand Dunes Bay) (FM792014)**Coral Community Type:** A, B (site number 135)**Description:** *Porites* boulders fringe the south shore, fusing about midway out to form a solid flat-topped framework reef 1-2m thick; reef changes considerably moving east toward mouth of bay: banks of *P. damicornis* appear along reef edge in 4-5m depth; *Porites* gives way to talus slope covered by small (10-15cm) bushy *Acropora*; further out talus and boulder platform is covered by *Montipora* with a mixed coral assemblage along the seaward margin in 6-7m depth; from here reef detaches from shore and is covered >85% by alcyonarians (*Sarcophyton* predominant); this leads to mixed coral assemblage.**Threats:** ropes, gill net in coral.***Ra's Khayran (East Sand Dunes Bay)*** (FM794014)**Coral Community Type:** B (site number 136)**Description:** shoaling rock shelving north to sand at 12m, dropping steeply seaward to 13m, and falling over walls, ledges, overhangs south; rock terraces covered 70-95% corals and *Sarcophyton*, cut by sandy gullies.**Threats:** ropes, net in coral; spearfishing.***Khaysat Ash Shaykh East*** (FM796006)**Coral Community Type:** B (site number 137)**Description:** rock slope covered by fine algal turf and scattered alcyonarians and corals.***Khaysat Ash Shaykh Southeast*** (FM798008)**Coral Community Type:** B (site number 138)**Description:** cliffs fall to terrace at 7m with algal turf and dense *Echinostrephus molaris* with few corals; area of large blocks rock tumbled together with a variety of corals; off east side rock slopes to 18-21m where rocky patches covered by gorgonians.**Threats:** intense gill net fishing; ropes in coral.***As Sifah North*** (FM816972)**Coral Community Type:** B (site number 139)**Description:** rocks covered by short algal turf and scattered small corals; *Symphyllia* common.***As Sifah*** (FM844885)**Coral Community Type:** B (site number 140)**Description:** boulder-strewn seabed with predominantly faviid corals and alcyonarians out from ca. 1m below low tide mark.**Threats:** intense shell and lobster collection by expatriates.***Ra's Abu Da'ud (Islet)*** (FL960800)**Coral Community Type:** A, B (site number 141)**Description:** sheer wall north side islet with small encrusting corals, and abundant *Tubastrea*, *Dendrophyllia*, *Dendronephthya* and gorgonians; south of islet are several large banks of dead coral (2-3m thick) with recolonisation by small (8cm) colonies of *P.*

damicornis, *Acropora*, *Stylophora* (5-25% cover only); rock slopes toward southeast end have mixed corals reaching 50% cover.

Threats: gill nets entangled in and killing coral and large gastropods; coral breakage; spearfishing; *A. planci*, 2 seen exposed.

Bimmah North (GL185450)

Coral Community Type: B (site number 142)

Description: rock shelf 4-7m deep, *Sarcophyton*, *Sinularia* predominant with scattered corals, including large *Turbinaria*, *Platygyra*.

Makalla Wabar (GL282337-293304)

Coral Community Type: B (site number 143)

Description: north side beach GL282337 rock shelves and ridges angle off shore to depth 3-6m; 6m shelves have alcyonarians (*Sarcophyton*, *Sinularia*) predominant with scattered small corals; shallower ridges have greater cover hard corals (*Acropora*, *P. damicornis* predominant); ca. 500m offshore in 11-12m depth GL287325 is low rock shelf with numerous small scattered corals, alcyonarians, and few large *Astreopora* and *Porites*; *Turbinaria peltata* and *Pseudosiderastrea* common and relatively large; east side headland GL293304 cliff drops to terrace at 9m dropping sheer to sand at 12m, north side rocky slope (gradient 1:1) to sand 9m; small scattered corals; *Sarcophyton*, *Sinularia* predominant.

Threats: fishing lines in corals.

Ra's North Qalhat (GL380185)

Coral Community Type: B (site number 144)

Description: rock platform at 5-6m depth cut by sheer-sided gullies with alcyonarians and scattered corals (usually <50cm colonies).

Wadi Birka Area (GL494072)

Coral Community Type: B

Description: west of wadi a series of rock shelves run parallel to the shore out to at least 10m deep; shelves notably barren, supporting few scattered corals, cover <1% nearshore (2m depth) increasing offshore to 1% in 3-4m, 5-7% in 7-8m, and 10% in 9-10m; proportion dead corals remains 5%; opposite wadi rock shelves raised 1-2m above sandy substrate, 2% cover in 4-5m (20% dead), 5-10% in 6m (<2% dead, tabular *Acropora* predominant), 70% cover in 9m (3% dead, mixed corals and alcyonarians); large *Porites* heads (some >4m diameter) occur just east of the wadi.

Threats: gill nets in coral; tarballs, litter, trash and sewage from Oman Sea Farms in wadi and sea; effluent from prawn ponds enhanced algal growth and apparently killed or killing 82% of *Porites* colonies of >1m diameter near outfall.

Bi'r Bira' West (GL520045)

Coral Community Type: A, B (site number 145)

Description: coral cover 60-70% in continuous band ca. 100m offshore GL520045-544025; *Montipora*-*Acropora* dominated framework reef (>1m thick) with spur and groove

formations from 3-6m depth; coral cover decreases gradually to 50% in 6m then drops rapidly to 10% in 8m, 5% in 9m and 2% in 10m; shallows predominantly *Sarcophyton*, *Sinularia*, *Tridacna*, *Lambis*, *Euphyllia* and other corals on gravel terrace above beach, but none underwater.

Threats: gill nets in coral, overturned *Acropora*; land allocated for desalination plant with 1km sea frontage opposite west end this well-developed and only coral reef in the area (GL520045).

***Bi'r Bira'* (GL533033)**

Coral Community Type: A, B (site number 146)

Description: eastern extension of reef described in previous record; coral cover increases to maximum of 80% towards east before breaking apart ca. 200-300m east of Bi'r Bira'.

Threats: ropes, gill nets in coral; collection *L. truncata*.

***Khawr South of Shiya* (GK755959)**

Coral Community Type: B (site number 147)

Description: scattered small coral colonies on rock.

***Khawr Jaramah* (GK810910)**

Coral Community Type: A, B

Description: Young reefs, much dead coral.

***Barr al Hikman Southeast* (FH520520)**

Coral Community Type: A, B (site number 148)

Description: *Platygyra-Porites* dominated reef with huge heads forming 100% cover in patches, and large patches whorled *Montipora foliosa* and *Acropora*; generally mixed low diversity coral assemblage; unlike reefs elsewhere in Oman; reef extends southeast of Ra's al Mishayu 100x4500m; 4May87 *Sargassopsis* up to 45cms long, dense *Sargassopsis* reef-flat southeast.

Threats: occasional gill net fishing by fishermen from Al Ashkharah; ropes in corals.

***Barr al Hikman (south reefs, east side)* (FH480500)**

Coral Community Type: A (site number 149)

Description: east part of the large (>6sq.km.) reef formed exclusively of *Montipora foliosa* - structure this series of reefs unique in Oman and possibly the world; largest continuous coral reef in Oman, extending FH510490-420530 (>10km); framework ca. 4m thick built of huge whorled *M. foliosa* (cover 100% over flats); where few open pools in reef find small selection of other corals; seaward margin (south-facing) protected from waves by talus banks formed of broken, dead pieces of *M. foliosa* and low spurs of *P. damicornis* off the reef edge in 3-5m depth; inner margin shallow (0.5-1.5m deep low neap tide), irregular contours of mounds and ridges; leads offshore to broad flat zone 70:30 live:dead coral.

Barr al Hikman (Ra's Ghabirty West) (FH420528)**Coral Community Type:** A (site number 150)**Description:** western limit of unique vast *M. foliosa* reef complex (see previous record for more details); off west edge reef fragmented patches *M. foliosa* and large *Porites* and *Platygyra* with small colonies other corals in 2-3m over sand.**Ra's Kanasah (coral shoal south) (FH270530)****Coral Community Type:** B (site number 151)**Description:** shoal with coral patches (>50% dead) with scattered faviids predominant; edge with bank of *M. foliosa* west, *Porites* boulders north.**Ra's Shajrit (FH244594-246600)****Coral Community Type:** B (site number 152)**Description:** rock reef fringes shore; prolific coral growth (70% cover) FH245580; *Platygyra*, *Porites*, *Hydnophora*, *Goniopora* predominant; further north rock boulders with faviids and *Sinularia*, live coral 30%, alcyonarians 30%, dead coral and rock 40%.**Threats:** gill net set among coral.**Jazirat Abb (FH215672)****Coral Community Type:** B (site number 153)**Description:** 2m deep rock shelf extends out from island with patches (100-1000 sq.m.) bushy *Acropora* between which are rocks with massive corals (mainly faviids).**Bandar Hasik West (CE190255)****Coral Community Type:** C**Description:** rock boulders with algal turf, scattered corals, including: *Montipora*, *Acropora*, *Pseudosiderastrea*, *Stylophora*, faviids; *Ulva*.**Ra's Hasik North (CE195245)****Coral Community Type:** C**Description:** coral more abundant than Bandar Hasik West; tabular *Acropora* 3-4m diameter, large spherical tunicates encrusting rocks.**Ra's Hasik South (CE195241)****Coral Community Type:** C**Description:** numerous small *Stylophora*, *Pseudosiderastrea*, encrusting *Montipora* in shallows, small tabular *Acropora* deeper.**Ra's Hasik South 1 (CE189235)****Coral Community Type:** C**Description:** bay bordered north and south by tumbled rock with short algal turf; *Ulva*; few scattered faviid corals south side; *Acropora*, *Stylophora* further out; *Tubastrea* 6m vertical face; *Dendrophyllia* 3m overhang; exposed north side more coral: patch small (<1m diam) *Acropora*, *Porites* <75% cover of rock.

Khawr Murir North (CD018939)**Coral Community Type: C**

Description: in bay rock with *Sargassopsis*, *Ulva*; outside strong surge scattered *Montipora*, *Acropora*, *Stylophora*.

Wadi Mahall North (BD995905)**Coral Community Type: C**

Description: *Acropora*, *Stylophora*, faviids; fewer than BD990900; *Sargassopsis* on shallow rock outer bay; *Ulva*.

Threats: lines in coral; litter underwater.

Wadi Mahall (BD990900)**Coral Community Type: C**

Description: south shore *Acropora*, *Stylophora*, faviids, *Turbinaria* in large sheets and *Favia* on rock wall in inner bay; *Sargassopsis* outer bay and north shore inner bay; *Ulva*.

Threats: lines in coral; much litter underwater.

Wadi Mahall South (BD986895)**Coral Community Type: C**

Description: many large *Porites* boulders (>1m diameter) along south shore, *Acropora*, *Montipora*, *Stylophora*; *Sargassopsis* on shallow rock; more coral here than north of Sath; *Ulva*.

Threats: abundant litter.

Sadh (BD949856)**Coral Community Type: C**

Description: boulders in shallows covered by stubby *Sargassopsis* with occasional small *Stylophora*; below 8m scattered *Acropora* and encrusting *Montipora*; *Ulva*.

Sadh South (BD941853)**Coral Community Type: C**

Description: large patch *Sinularia*; much *Eklonia* on tideline; north side bay rock with algal turf, to *Sargassopsis* from shallows to 6-7m, to rock with algal turf and occasional *Acropora*, *Stylophora* to sand centre bay; south side same zonation but greater abundance and variety coral including *Acropora*, *Stylophora*, *Montipora*, *Porites*, *Coscinaraea*, *Pseudosiderastrea*, *Cyphastrea*, *Favites* sp., *F. pentagona*; tabular *Acropora* (<1m diameter); cover reaching 30% in patches; *Ulva*.

Sadh South 1 (BD932846)**Coral Community Type: C**

Description: rock with algal turf-*Sargassopsis* to 6-7m, to algal turf and occasional *Stylophora*, *Acropora*, to deeper turf with flat calcareous rhodophytes; centre bay sandy; south side more, bigger corals than BD941853, same corals and *Acanthastrea maxima*; *F. pentagona*, *Cyphastrea*, *Acropora* reach >1m diameter; *Ulva*.

Wadi Khorhaufa North (BD923841)**Coral Community Type: B**

patchy coral (*Montipora*-*Porites*-*Cyphastrea*-*F. pentagona* dominant) 8-10m in more exposed parts of bay.

Wadi Khorhaufa (BD914835)**Coral Community Type: C**

Description: *Sargassopsis*, patchy *Acropora*, *Cyphastrea*, *F. pentagona* on south side; *Ulva*.

Ra's Janjali Northeast (BD900828)**Coral Community Type: C**

Description: Inner bay very sheltered; rock with *Padina*, numerous *Echinometra*; outer bay *Sargassopsis*, *Favites* sp., *F. pentagona*, *Acropora*; *Ulva*; below this zone larger colonies coral including *Montipora*, *Cyphastrea*, 4+m diameter *Leptastrea* with 11 slipper lobsters underneath.

Bandar Qinqari East (BD891827-890812)**Coral Community Type: C (site number 155)**

Description: below 6m *Acropora*, *Montipora*, faviids in exposed location 15-20% cover; at 10m 30-40% cover with blunt-branch *Porites*, *Turbinaria*, *Platygyra*, *Cyphastrea*, *Leptastrea* (>2m diameter), *H. exesa*; *Sargassopsis* shallower; *Ulva*.

Wadi Bayt Said East (BD828795)**Coral Community Type: A, C (site number 156)**

Description: Tiers tabular *Acropora* (2-3m diameter) east side from 3m to 6-7m deep, 75% cover, large *Porites* (2m diameter, with 1 of 4m); further out bay rock terrace 9m deep with dense coral cover down to sand 13m; similar west side but coral band narrower.
Threats: lines in coral.

Wadi Bayt Said West (BD782790)**Coral Community Type: C**

Description: generally algal turf with *Padina* inner bay; sparse *Sargassopsis*, scattered *Stylophora* outer bay with small tabular *Acropora* deeper; large area coral 20-30% cover in cove at mouth east end BD793784; large heads *Porites*, *Cyphastrea*, tabular *Acropora* scattered along rocky borders of cove BD790789.

Wadi Aingalf East 3 (BD756770)**Coral Community Type: A, B, C (site number 157)**

Description: cover 40-60% from 6 to 15m.

Threats: lines in coral.

Wadi Aingalf East 2 (BD752769)**Coral Community Type: A, B, C (site number 158)**

Description: gradual slope (gradient 1:5) with coral from 5-6m to bay floor 10m; at 6-7m

Acropora-Montipora assemblage cover 80-90%, 9-10m coral cover 50-80%; definite reef framework; inner bay *Acropora-faviid* assemblage at 5m.

Threats: lines in coral.

Wadi Aingalf East 1 (BD748767)

Coral Community Type: A, B, C (site number 159)

Description: See BD746773 for inner bay; corals begin 8m, terrace at 9m with gentle slope to 15m with 60% cover coral in patches, extend down sides, ends rock ridges to 17m; some patches dominated by large *H. exesa* or *Pavona* or *Echinophyllia*.

Threats: gill net, lines in coral.

Wadi Aingalf East (BD746773)

Coral Community Type: C (site number 160)

Description: See BD748767 for details outer bay; rock with algal turf to 8m; east side 8m down *Acropora*, *Cyphastrea*, *F. pentagona*, cover 5-50%; tabular *Acropora* predominant; west side less coral; *Ulva*.

Wadi Ayn East (BD727766)

Coral Community Type: A, B, C

Description: west side few scattered corals outer bay, huge *Porites* (3-4m diameter, one 4-5m) in 2-4m depth inner bay; centre bay patch reef formed on sand of large *Porites* fused together, other corals where *Porites* dead; east side <20% cover coral encrusting rock slope, patchy.

Threats: lines, gill net in coral.

Wadi Ayn (BD724768-726765)

Coral Community Type: B, C

Description: rock with silty algal turf-*Stylophora-Acropora-Porites* from 2m to sand 7m where much *Padina*; further out gullied rock with sides, rocky bottoms gullies coral encrusted (predominantly table *Acropora*); *Ulva*.

Wadi Ayn West (BD709768)

Coral Community Type: A, B, C

Description: small patch reef; rock with algal turf-*Sargassopsis*-? *Dictyota*, *Ulva*, occasional *Stylophora*, *Acropora*, faviids increasing in abundance in centre bay; toward west-centre bay coral cover 40-60% at 8m; in mouth bay, rocks bay floor corals fewer; large patches *Sinularia*.

Raaha (Hoon's Bay) East (BD664749)

Coral Community Type: A, B, C (site number 161)

Description: Bay sheltered by shallow rock spur across mouth; true reef framework, extensive coral growth extending to outer bay on 9m terrace; inner bay shallow algal covered coral; much *Sargassopsis* outer; *Ulva* (see next record for west side bay).

Threats: lines, ropes in coral; coral heads used to weight fish traps; spearfishing, broken coral, tarballs, litter underwater; litter ashore, oil on rocks.

Raaha (Hoon's Bay) West (BD663747)**Coral Community Type:** A, B, C (site number 162)**Description:** true reef framework with cover up to 99%; 3m terrace dominated by *Acropora*; reef developed over terrace, down rock slope to 10m; large *Porites*, *Pavona* heads (2-5m diameter); further out rock spur with dropoff to 12m, *Stylaster* abundant.**Threats:** lines in coral; broken coral, selective spearing groupers.**Raaha West 1 (BD660747)****Coral Community Type:** A, B, C**Description:** Inner bay: patchy scattered coral on rock 5-40% cover, primarily *Acropora*, large *Platygyra*, branching *Porites*; outer bay east side: small patch branched and massive *Porites* forming veneer framework, 95% cover live coral on rock slope and smaller less consolidated patches *Pavona*; outer bay west side: stepped rock shelves, ledges, cover 0-60%, primarily *Platygyra* and branched *Porites*, decreasing from outer to inner bay.**Raaha West 2 (Eagle's Retreat) (BD654743)****Coral Community Type:** B, C (site number 163)**Description:** algal turf-*Sargassopsis* and scattered *Acropora*-*F. pentagona* on rock outcrops closer to shore and few *Montipora*, encrusting *Porites*; crevices packed *Echinometra*, *Stomopneustes*, large tunicates, large octopi; further offshore outcrops from sand at 5-10m depth to 3m deep running parallel shore from rock islet at north end; coral encrusted spurs, gullies south small beach; further out tumbled rock slope with large *Turbinaria*, patchy tiers tabular *Acropora* 5-9m; shown fungiid allegedly found here.**Threats:** lines in coral; coral broken by divers.**Raaha West 3 (BD650749)****Coral Community Type:** B, C**Description:** tumbled rock with scattered *Acropora* (predominant), *Turbinaria*, smaller colonies faviids; cover <5% increasing in inner bay to 20-30% with predominantly massive corals (*Porites*, *Goniopora*, *F. pentagona*), *Stylophora* in 1.5-3m; east side rock scoured bare.**Threats:** lines in coral.**Wadi Anshayr East (BD611766)****Coral Community Type:** A, B, C**Description:** east side large *Porites* patch reef >2m thick, 40% live coral cover - rest dead coral (not rock!); *Porites* heads (1-1.5m diameter) scattered through cove and in shallows; rocks with scattered *Acropora*, faviids, *Coscinaraea*; shallows *Porites* forms reef framework up to 1m thick; *Ulva*.**Khawr Hino West (BD601760)****Coral Community Type:** B, C**Description:** rock slope 1:3 gradient, corals patchy, scattered; cover to 70% in 1 patch; *Acropora* predominant on sides, bottoms gullies; inner bay sand-rock pavement; few small corals.

Hino South (BD596760)**Coral Community Type: C**

Description: shallow rock with silty algal turf, turbid water with decaying algae; at 2m algae with few scattered small corals (*Stylophora*, *F. pentagona*); at 3-4m scattered *Acropora*, *Favia*, *Favites*, *Cyphastrea*, *Goniopora*; *Sargassopsis*, *Ulva*; 50cms deep *Sargassopsis* on tidelines 25Aug88.

Jazirat Hino West (BD594755)**Coral Community Type: B, C** (site number 164)

Description: shallow rock around island with *Sargassopsis*, scattered corals to 4-5m; below this more coral; coral more abundant west side: rock slope edge channel 40-60% cover, reaches 90% centre west bay, huge *Porites* (12m diameter 3m thick); 24Aug88 mainland shore piled 50cms thick *Sargassopsis*; *Ulva*.

Threats: coral heads used to weight fish traps.

Marbat South (BD545780)**Coral Community Type: C**

Description: rocky outcrops with scattered coral, predominantly tabular *Acropora*, large *Turbinaria*, faviids, 2% cover; large sand patches.

Ra's Marbat (BD530786)**Coral Community Type: B** (site number 165)

gullied rock with algal turf, scattered coral, 2% cover, including unusual deeper water varieties.

Marbat (BD536793) A, C

Description: small incipient patch reef formed fused *Porites* colonies, 2-3m diameter (S-centre cove); centre cove rock outcrops with scattered *Acropora*, *Montipora*, faviids, occasional large *Platygyra* (1-2m diameter), *Porites*; *Porites* generally <1m diameter but larger, more abundant under lee south rock point (1-2m diameter); bay floor rock with algal turf, small sand patches, scattered coral; fewer corals north side cove.

Threats: lines, gill net in coral.

Ra's Raysut (Raysut Rock) (AD815749/ZU208749)**Coral Community Type: C** (site number 166)

Description: east side: rock shelf 9-12m gradual slope, sheer-stepped to >16m with overhangs, shallow caves; south side: more scenic with sandy gullies, caves to sand at 15-16m; rock with short algal turf, scattered encrusting corals, tunicates; deeper caves/overhangs south side with black coral (*Antipathes* sp.) - killed by entangling lines/ropes in places; few coral types.

Threats: ropes, lines tangling marine life, killing antipatharians; old ropes, fishing lines, litter underwater.

Raysut West (Rock Stack) (ZU190740)**Coral Community Type:** B (site number 167)**Description:** rock blocks, gullies with short algal turf, scattered corals <5% cover.**Threats:** lines in coral.***Raysut West 1*** (ZU173730)**Coral Community Type:** B**Description:** rock outcrops with short algal turf, scattered encrusting corals, generally 5-15% cover, 25% maximum; *Ulva*.***Ra's Hamar*** (ZU140710)**Coral Community Type:** B (site number 168)**Description:** steep rock terraces 9-12m deep with short algal turf, scattered coral; gravel-shell talus down slope with corals, other encrusting organisms; cave at 15m below which sand-rock slopes steadily deeper.**Threats:** lines in coral, rock.***Fizayih*** (YU892631-888625)**Coral Community Type:** B (site number 169)**Description:** sides rock outcrops encrusted by coral, scattered corals top; north side point sheltered, luxuriant coral patches, 50-90% cover (*Platygyra* <2m diameter).***Ghubbat al Fizayih West*** (YU846574-850584)**Coral Community Type:** B (site number 170)**Description:** YU852576 large rock blocks, caves, narrow sheer-sided gullies, encrusted corals, abundant large fishes (including large spotted *Dermatolepis*), *Echinostrephus*, seafans, some black coral; sides gullies/overhangs encrusted *Tubastrea*, *Styaster*.**Threats:** lines in coral.***Ra's Sajir East*** (YU795555)**Coral Community Type:** B**Description:** flat rock encrusted 25% with *Montipora* increasing to 50% on rock boulders, outcrops where *Montipora*, tabular *Acropora*, faviids, *Pavona* (massive, untidy), *Leptastrea*, *H. microconos*; *Echinostrephus* exceedingly abundant.***Wadi Nhaart East (Millepora Bay)*** (YU710544)**Coral Community Type:** B (site number 171)**Description:** large boulders nearshore to rock shelves, outcrops with abundant coral; coral cover 25-50% maximum; corals encrust rock with *Platygyra* as low colonies >1m diameter; corals seen include table *Acropora*, *Platygyra*, *Montipora*, *H. exesa*, massive blade *Pavona*, *Porites*, *Millepora*; *Millepora* and scattered corals down to 5-6m; at 6-9m variety corals to 25% cover; 9-15m *Echinopora* predominant, <65% cover.

Ma'alqawt* (YU700546-693548)*Coral Community Type:** B (site number 172)**Description:** rock ridges, gullies, outcrops with algal turf, scattered corals.***Kharfot* (YU488508)****Coral Community Type:** C (site number 173)**Description:** Offshore at 12m deep 90% cover *Sargassum* with small rock shelves with sponges and very small scattered corals.***Shinays* (DE087477)****Coral Community Type:** B**Description:** Bare rock and rock with strips *Sargassopsis*; scattered small colonies *Stylophora*, *Porites*, *Acropora*, *F. pentagona* and other faviids, *Montipora*.***Al Hallaniyah (Northwest Bay)* (CE900364)****Coral Community Type:** B, C (site number 175)**Description:** Bay bordered by rock, encrusting coral; extensive coral gardens south side; occasional huge *Porites*; sandy seabed with rock ridges, dominates, coral-encrusted or with *Sargassopsis*, coral cover 0-75% live.**Threats:** gill net in coral.***Al Hallaniyah Southeast* (DE032355)****Coral Community Type:** A, B, C (site number 176)**Description:** Extensive coral in bay, banks *Stylophora* in sheltered coves, *Porites* heads in solid fused banks; tiers *Acropora*; rocky slopes covered by variety smaller coral colonies; some areas coral cover 99% live; breeding area *Chaetodon vagabundus* and *Megaprotodon strigangulus*.**Threats:** net in and breaking coral.***Al Hallaniyah South 2* (CE929338)****Coral Community Type:** B, C (site number 177)**Description:** Inner bay: boulders with luxuriant *Sargassum*, scattered bushy and tabular *Acropora*, *Porites*; further out vast tabular *Acropora*, *Porites* (some fused) and *Platygyra*; outer bay: depth 7-8m, more varied corals, occasional large *Porites*; <99% cover; vertical walls *Tubastrea*, *Echinophyllia*, *Blastomussa*.***Al Hallaniyah (Southwest Bay)* (CE911342)****Coral Community Type:** A, B, C (site numbers 178, 179)**Description:** Inshore large boulders with luxuriant algae, small colonies corals *Porites*, *Montipora*, *F. pentagona*; large shoals scarids, carangids, siganids, *Diplodus*; 6m shelf 90% coral cover (50:50 hard:soft); coral reef dominated by extensive spur fused *Porites* 1-1.5m thick, 100% coral cover, 70-80% live.**Threats:** net in and breaking coral.

As Sawda (CE780350)**Coral Community Type:** A, B, C (site number 180)**Description:** reef framework west bay.**As Sawda Northeast (CE808346)****Coral Community Type:** B, C (site number 181)**Description:** Tabular *Acropora* forms large patches 70-90% live coral in tiers; patches *Porites* (>2-3m diameter) with bushy *Acropora*, *Platygyra*, large *Goniopora*, *Turbinaria*; coral extends out of bay to sides/bases rock spurs, where smaller, more varied colonies.**As Sawda East (CE808334)****Coral Community Type:** A, B, C (site number 182)**Description:** Scattered *Porites* in bay, and bushy *Acropora*; *Porites* heads further out and encrusting coral; extensive tiers tabular *Acropora*, large dead area; outer bay much live coral, dropoff to coral-covered floor at 12m.**As Sawda South (CE781336)****Coral Community Type:** A, B, C (site number 183)**Description:** Coral scattered over shallower rocks; framework (<1m thick) fused *Porites* in sheltered west coves; bay floor 6-13m <80% coral cover over vast area; deeper corals dominated by large *Echinopora* (about 50%), *Montastrea curta*; *Millepora* along rock fringe; extensive tiers tabular *Acropora*.**As Sawda (West Bay) (CE758344)****Coral Community Type:** A, B, C**Description:** bay lined by *Porites* (boulders, knobbed, branching), forms 1-2m thick framework platform along south shore, dead on top; banks largely dead coral centrally with small *Stylophora* (30-95% dead); north side much dead branching coral, *Porites* in outer reaches, inner part *Porites-Turbinaria* (alga), numerous *Goniopora* colonies; large 2-4m diameter *Acropora* tables, *Porites* boulders at mouth bay.**As Sawda Northwest (CE760350)****Coral Community Type:** B, C (site number 184)**Description:** west side inner bay *Stylophora* forms wide flat "micro-atolls" and few small *Porites*; bay floor sand, small rock boulders; several dead very large table *Acropora*, much live table *Acropora* west side near headland; rock boulders off west headland covered (50-80%) corals, mainly table *Acropora* (2-3m diameter), *Platygyra*.

APPENDIX 3. SUMMARY OF CORAL BLEACHING OBSERVATIONS, MUSANDAM (grid coordinates from National Survey Authority Map Series K6611, 1:100,000)

Jazirat Habalayn (DP357938):

Air Temperature:

22/07/90 39°C (1400 hrs).

Sea Temperature:

22/07/90 34.5°C (1400 hrs) at surface to 1 m depth, gradually cooling to 32°C at 10-12 m.

25/08/90 33°C (1430 hrs) at surface; 32.5°C at 5 m; 32°C at 8 m.

20/10/90 30°C (1530 hrs) at surface.

Observations:

22/07/90 Colonial zoanthids bleached white; minor bleaching of some *Acropora*, *Montipora*, and *P. cactus* to noticeably pale, but not white.

25/08/90 All *Stylophora* bleached to pale yellow, and all *Acropora* and zoanthid *Palythoa* to bright white; some *Porites*, *P. cactus*, *Echinopora*, and anemones bleached white, and *Astreopora* pale blue. Exposed horizontal surfaces of coral colonies more bleached than vertical or shaded ones.

20/10/90 Corals largely recovered, but picture confused by *Acanthaster* predation. *Palythoa* dead, discoloured and sloughing off rock; *Symphyllia* and anemones remain bleached but alive and responsive to stimulus; <20% *Stylophora* and *Acropora* in shallows dead and covered by fine filamentous alga; remaining *Stylophora* and *Porites* have recovered normal colouration, showing no sign of bleaching; 80% *Echinopora* still bleached, 30% dead; 50% *P. cactus* dead.

Jazirat Maqlab (DP344974):

Air Temperature:

26/07/90 38°C (1200 hrs).

22/08/90 39°C.

21/10/90 34°C.

Sea Temperature:

26/07/90 33°C (1200 hrs) surface to 1 m; gradually cooling to 31°C at 10-12 m.

22/08/90 33.5°C at surface; 32.5°C at 12 m.

21/10/90 30°C surface to 10 m.

Observations:

- 26/07/90 No sign of coral bleaching.
- 22/08/90 Fine-branched *Acropora* severely bleached all around island; patchy bleaching of stout-branched *Acropora*, and table *Acropora*; *Montipora* and *P. damicornis* bleached white; some *P. cactus* bleached to pale yellow-brown.
- 21/10/90 Extensive bleaching-related mortality to *Acropora*; fine-branched *Acropora* 60-90% dead from patch to patch; stout-branched *Acropora* <2 m depth 60% dead, >2 m depth largely unaffected, but some patches 75% dead down to depth of 5 m; table *Acropora* about 25% dead; *P. damicornis* 12% dead (only one large colony present). *P. cactus*, *Porites*, *Platygyra*, and all other corals have recovered normal colouration.

*Jazirat Sibi (DQ391001):**Air Temperature:*

- 22/08/90 39°C.
- 21/10/90 34°C.

Sea Temperature:

- 22/08/90 34°C surface to 1 m; gradually cooling to 33°C at 10 m.
- 21/10/90 31°C surface to 3 m.

Observations:

- 22/08/90 Extensive bleaching of fine-branched *Acropora* down to 3 m depth; stout-branched *Acropora* patchy bleaching; table *Acropora* little affected; *Stylophora* bleached; no bleaching below 5 m depth. Bleaching variable from pure white to pale yellow, with upper parts of branches paler than shaded lower sides. Some branched dead and covered by sparse cover of fine filamentous alga.
- 21/10/90 Only *Acropora* shows mortality. *Acropora* mortality down to 3 m depth averages about 80%, with patches of fine-branched, stout-branched and tabular species all affected. Mortality varies between 60% and 98% from patch to patch. *Pavona*, *Porites*, and faviids all have normal colouration.

*Khawr Quway' (DQ365160):**Sea Temperature:*

- 22/08/90 32°C (1400) surface to 6 m.
- 21/10/90 29°C (1300) surface to 1 m.

Observations:

- 22/08/90 NE side shelf below small beach: *Porites* over reef-flat bleached to yellow or pale blue, extensive but not severe; some zoanthid *Palythoa* colonies bleached to pale yellow-brown with dead patches turned green by epiphytic alga.
- 24/08/90 W side along Jazirat Umm al Ghanam: luxuriant *Acropora* and *Montipora* reef with extensive bleaching of *Montipora*, but *Acropora* unaffected. Colour of bleached *Montipora* grades from pale brown to near white or very pale blue.
- 21/10/90 Some mortality of table *Acropora* (<1%) that may be bleach related. All other corals show normal colouration, including the formerly badly affected *Montipora*.

*Maqaqah (DP376977):**Sea Temperature:*

- 25/08/90 35°C surface; 34°C at 3 m.
- 20/10/90 31°C surface to 3 m.

Observations:

- 25/08/90 Branching *Acropora*, *P. cactus*, *Leptastrea*, *Favia*, *Favites* and *Platygyra* all bleached to pale yellow or white. Some *Platygyra* dead and covered by sparse fine filamentous alga and sediment deposit. *Porites* unaffected.
- 20/10/90 *Favia* and *Favites* recovered from bleaching. *P. cactus* about 10% dead and some still bleached but apparently recovering; *Platygyra* 30-40% dead, mostly on dorsal surface which now covered by alga and silt.

*Nibah (DP430854):**Sea Temperature:*

- 20/10/90 29°C at surface.

Observations:

- 20/10/90 Minimal bleaching of *Echinopora* and *Favites*. No other corals affected, no mortality.

*Ra's Marovi (DP432742):**Sea Temperature:*

- 20/10/90 29°C at surface.

Observations:

20/10/90 No evidence of bleaching.

*Zaghi South (DP276417):**Sea Temperature:*

20/10/90 31°C (0900 hrs) surface to 5 m.

Observations:

20/10/90 Table *Acropora* 90-95% dead above 3 m depth; below 3 m 95% alive; *Platygyra* 1-2% bleached and dead, many alive but dorsal surface bleached to pale brown; *Symphyllia* bleached to pale yellow but alive.

*Ra's Sawt (DP279410):**Sea Temperature:*

20/10/90 31°C (0930 hrs) surface to 5 m.

Observations:

20/10/90 All *Sinularia*, and some *Symphyllia* and *P. damicornis* bleached but alive; about 1% of *Platygyra* bleached and dead. In the outer bay all corals healthy. In the inner bay all table *Acropora* shallower than 3 m was dead, patches at 3 m 20-50% bleached.

ATOLL RESEARCH BULLETIN

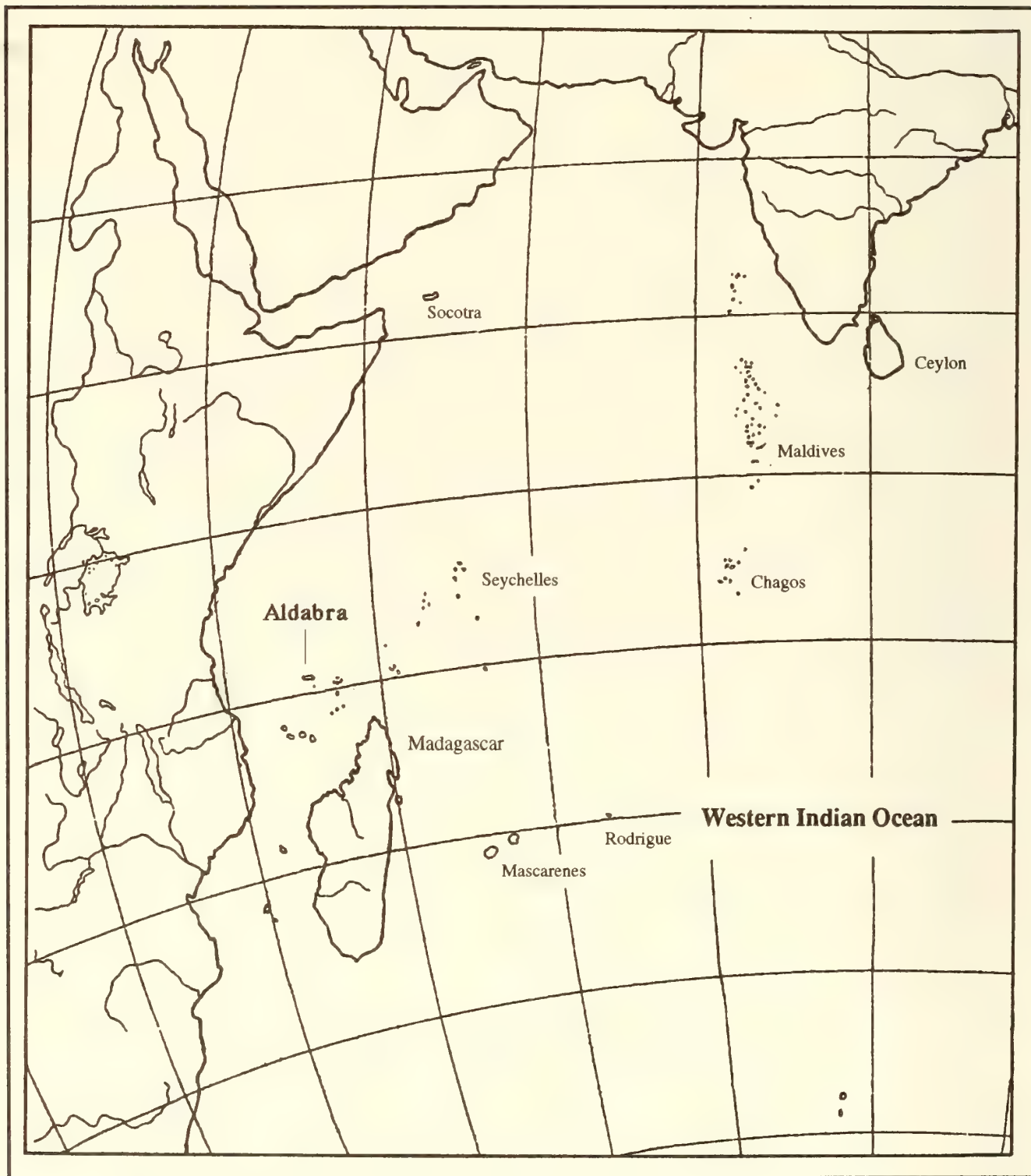
NO. 381

**THE HETEROPTERA OF ALDABRA ATOLL AND NEABY ISLANDS,
WESTERN INDIAN OCEAN, PART 2. FRESHWATER HETEROPTERA
(INSECTA): CORIXIDAE, NOTONECTIDAE, VELIIDAE,
GERRIDAE AND MESOVELIIDAE**

BY

DAN A. POLHEMUS

**ISSUED BY
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ABSTRACT

Five species of freshwater Heteroptera are now recorded from Aldabra Atoll. Two of these species, *Micronecta praetermissa* and *Anisops vitrea* are subaquatic species living below the water surface, while the remaining three, *Mesovelina vittigera*, *Limnogonus cereiventris* and *Microvelia diluta diluta* inhabit the water surface. The latter species also inhabits saline limestone sinkholes that are flooded on a daily basis by tidal fluxes. A key to all these freshwater species is provided, accompanied by discussions of their habitat preferences and maps detailing their distributions on Aldabra.

INTRODUCTION

This is the second in a series of reports on Heteroptera fauna of Aldabra and nearby Indian Ocean atolls, and deals with those species of Heteroptera occurring in freshwater habitats. The diverse marine Heteroptera fauna of Aldabra was treated in a previous report (Polhemus, 1990), which also contained a detailed description of the atoll and its physical setting. The aim of these reports is to provide accurate information on the taxonomic composition, local distribution, and behavior of the Aldabran Heteroptera fauna that may be used by subsequent researchers at the Aldabra Research Station, particularly ecologists who need reliable taxonomic information on which to base their studies. It is further hoped that these contributions will be of use to entomologists and zoogeographers concerned with the distribution of insects in the Indian Ocean region as a whole.

The collections which form the basis for this report were made on Aldabra between March 9 and March 25, 1989, and during a one day stop on Cosmoledo Atoll on March 27, 1989, as part of a continuing research effort sponsored by the Smithsonian Institution's Aldabra Program in cooperation with the Seychelles Islands Foundation. The work on Aldabra was based primarily out of the research station on Picard Island, but an attempt was made to secure collections from most areas of the atoll. The collections from Cosmoledo were made primarily near the Johannes Point settlement on Menai Island, at the western end of the atoll. Given the relatively short time spent on these islands it is likely that further additions to their heteropterian faunas will be made by future collectors, and the present work should by no means be viewed as comprehensive. This report will, however, provide an updated basis from which subsequent workers may proceed.

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The last monograph of any scope to deal with the freshwater Heteroptera fauna on the atolls of the western Indian Ocean was that of Distant (1913), based on collections made by J. C. F. Fryer during the Percy Sladen Trust expeditions from 1908 to 1909. Many of Distant's taxonomic names and interpretations are now dated, and no publications dealing with the freshwater Heteroptera of this region have appeared since.

In reporting distributional data I have used the French names for the individual islands and channels of Aldabra and Cosmoledo atolls, since these are the names most commonly employed by the local Seychellois population. The French names have the following English equivalents that will be found on certain maps: Picard = West Island; Grande Terre = South Island, Malabar = North Island; Grande Passe = Main Channel; Passe Houareau = Eastern Channel; Passe Femme and adjacent passes = Western Channels. A detailed map of Aldabra showing these and other localities may be found in Stoddart and Westoff (1979).

The synonymies given under individual species are nomenclatural only. All specimens, unless otherwise noted, were collected by the author and are deposited in the National Museum of Natural History, Washington, D. C. CL numbers following collecting localities refer to a sequential numbering system used by the author to cross reference ecological data.

FRESHWATER HABITATS ON ALDABRA

The only permanent and unfailing source of fresh water on Aldabra Atoll is Wilson's Well, located on Grande Terre island near the head of Takamaka Arm. In addition, on the flat limestone surfaces or "platin" that occur widely across the atoll there are numerous shallow limestone pans or "bassins" that fill with water on a seasonal basis after the passage of convectional storms. The ponds formed in these bassins can persist for many weeks at a time, particularly during the months of March and April in the relatively rainy period between the northwest and southeast monsoons. Amid the rougher and more heavily weathered microkarst surfaces of the atoll there are also many smaller cavities that fill with water during the rainy months and are exploited by various aquatic insects, notably mosquitos. Finally, the construction of shelter huts and rain cisterns at various points around the atoll has provided many new and relatively permanent freshwater container habitats that did not previously exist.

The five species of freshwater aquatic Heteroptera present on Aldabra have taken advantage of all of the potential habitats noted above. The relative absence of permanent freshwater aquatic environments has dictated that these aquatic species be dispersive opportunists which can diapause in the egg stage during dry periods and then quickly hatch and develop to exploit those bodies of standing water that do become available after the rains. The presently known Aldabran water bugs are thus adaptable generalists of African, Malagasy or Asian affinities with broad distributions in the Indo-Pacific or western Indian Ocean regions. All appear to utilize temporary freshwater pools, and none appear to be exclusively confined to the one area of permanent fresh water at Wilson's Well on Grande Terre Island.

During the period in which the collections for the present study were made Aldabra received unusually consistent afternoon rains from convectional storms, and as a result the freshwater habitats were numerous and extensive. At Wilson's Well the broad limestone basin surrounding the vertical well shaft had flooded to a depth of over a meter, partially inundating the surrounding clumps of sedges and giving the area the appearance of a reed lined pond. This favorable circumstance had been readily exploited by numerous species of Odonata and aquatic Coleoptera, which coinhabited the pond with the five aquatic Heteroptera species discussed herein.

In addition to the permanent water source at Wilson's Well, two other large

temporary pools were also sampled during the course of this study. The first was at Takamaka Grove, a half hour's walk south of Wilson's Well in the central portion of Grande Terre island. This pool was large and roughly circular, being perhaps 15 meters across and a meter deep, and lay in a rugged limestone basin with low cliffs approximately 1.5 meters high along the eastern side. Adjoining these cliffs was the Takamaka Grove itself, a stand of large and apparently quite old takamaka trees (*Calophyllum inophyllum*). On the western side the shore was composed of lower, smoother limestone eroded into numerous small potholes and set with clumps of the sedge *Fimbristylus cymosa*. The surrounding country was also dotted with many small rain filled potholes plus one broad but very shallow expanse of water in a limestone pan at Bassin Ibis. These more ephemeral habitats contained few aquatic insects outside of mosquito larvae and *Microvelia*, in contrast to the pool at the grove which supported a diverse aquatic insect fauna.

A second large temporary pool was found several hundred meters inland from the camp at Cinq Cases, on the eastern tip of Grande Terre island. This was a broad expanse of water in a shallow limestone basin with low vertical sides no more than half a meter high. The water at this locality was almost entirely unshaded, and the extreme heat and glare during the daylight hours appeared to prevent most aquatic Heteroptera species here from venturing into the central section of the pool. They congregated instead along the margins, where some degree of protection was offered by small rock overhangs and clumps of the sedge *Fimbristylus ferruginea*. The pool substrate was composed of a thick layer of green, flocculant ooze suspended above the limestone floor, and the water contained numerous shells from dead giant tortoises which had fallen in and drowned while attempting to drink. Despite these conditions, this pool contained a rich freshwater aquatic biota, including all the species of freshwater aquatic Heteroptera presently known from Aldabra.

SYSTEMATICS

KEY TO THE ADULTS OF SPECIES OF FRESHWATER HETEROPTERA OCCURRING ON ALDABRA AND COSMOLEDO ATOLLS

1. a. Antennae shorter than head, inserted beneath eyes, not plainly visible from above; bugs living below the water surface (figs. 6, 7).....(*Nepomorpha*)..2
 b. Antennae longer than head, inserted forward of the eyes, plainly visible from above; bugs living on the water surface (figs. 8-10).....(*Gerromorpha*)..3
2. a. Beak triangular, very short, unsegmented, appearing as apex of head; front tarsus with a single segment, scooplike, fringed with stiff setae to form a rake; small brown species with body dorsoventrally flattened (fig. 6).....*Micronecta praetermissa* Poisson
 b. Beak cylindrical, longer than above, segmented, not appearing as apex of head; front tarsus not scooplike or fringed with stiff setae; larger pale colored species with body cylindrical (fig. 7).....*Anisops vitrea* Signoret
3. a. Claws on all legs inserted at tips of tarsi (fig. 9).....*Mesovelia vittigera* Horváth
 b. Claws of at least front tarsus inserted before apex.....4
4. a. Small species, legs short, with hind femur not surpassing apex of abdomen (fig. 8).....*Microvelia diluta diluta* Distant
 b. Much larger species, legs long, with hind femur greatly exceeding apex of abdomen (fig. 10).....*Limnogonus cereiventris* (Signoret)

CORIXIDAE

Micronecta praetermissa Poisson

Figs. 1, 6

Micronecta praetermissa Poisson 1938. Rev. Entomol., 5: 138. Type locality: Madagascar (Antanambé).

Discussion: This tiny waterboatman has a wider distribution in the western Indian Ocean than has previously been realized. In addition to the present specimens from Aldabra, I have collected this species in the dry forest regions of southern and western Madagascar (near Tulear and Morondava), and seen additional specimens from Zanzibar in the Hungerford collection at the University of Kansas. On Aldabra individuals of this species occurred abundantly in the large limestone pool inland from Cinq Cases camp on Grande Terre island, where they swam amid the flocculant green ooze on the pool bottom. Populations were also present in similar large pools at Wilson's Well and Takamaka Grove. It appears that on Aldabra *M. praetermissa* requires bigger pools of this type which persist for a long period of time, since it was not found in smaller, more temporary habitats such as rain filled pockets in the microkarst.

Known distribution: Madagascar, Zanzibar, Aldabra.

Material examined: ALDABRA ATOLL, **Grande Terre:** freshwater pool nr. Cinq Cases, water temp. 29° C., 13 March 1989, CL 8029; pool at Wilson's Well, water temp. 29° C., 23 March 1989, CL 8038; large pool at Takamaka Grove, water temp. 32° C., 23 March 1989, CL 8039.

NOTONECTIDAE

Anisops vitrea Signoret

Figs. 2, 7

Anisops vitreus Signoret (1860) 1861. Ann. Entomol. Soc. France, 8 (3): 972. Type locality: Madagascar.

Anisops aldabrana Distant 1913. Trans. Linn. Soc. London, Ser. 2, 16: 138. Type locality: Aldabra, Ile Michel. Syn. by Brooks 1951: 449.

Discussion: This small backswimmer was commonly encountered in freshwater pools on Grande Terre, and several specimens were also taken in a rain pool on Picard. In favorable situations this species often occurs in enormous schools, and individuals are easily observed as they hover just below the water surface.

Known distribution: Madagascar, Reunion, Mauritius, Aldabra.

Material examined: ALDABRA ATOLL, **Grande Terre:** freshwater pool nr. Cinq Cases, water temp. 29° C., 13 March 1989, CL 8029; pool at Wilson's Well, water temp. 29° C., 23 March 1989, CL 8038; large pool at Takamaka Grove, water temp. 32° C., 23 March 1989, CL 8039. **Picard:** temporary rain pool on trail to Bassin Cabri, 20 March 1989.

VELIIDAE

Microvelia diluta diluta Distant

Figs. 3, 8

Microvelia diluta Distant 1909. Ann. Mag. Nat. Hist., ser. 8, vol 3: 500.
Type locality: Bengal, Calcutta.

Discussion: *Microvelia diluta* is a widespread species in the Oriental region, and is also found on Aldabra and the Comores. We have no records of this species from Africa.

At my request a series of specimens from Aldabra was kindly compared by Dr. N. M. Andersen of the Zoologisk Museum, Copenhagen to the type series of *Microvelia diluta nioumbadjoui*, described by Poisson (1958) from Grande Comore. Dr. Andersen in his reply letter states that the Aldabra specimens clearly belong to the *M. diluta* group, but are smaller and less pilose than the Comores subspecies, being more similar instead to specimens of *diluta* from mainland Asia. In addition, it is Dr. Andersen's opinion that *M. diluta* as presently interpreted may in fact be a complex of closely related species. Pending resolution of this problem it seems most expedient for the present to treat the Aldabra and Cosmoledo populations as belonging to the nominate subspecies.

This resourceful species was encountered in nearly every freshwater habitat on the atolls of the Aldabra Group. It frequently colonized the plastic barrels used as rainwater cisterns at the small camps scattered about Aldabra, and was extremely common on the large freshwater pool at Takamaka Grove. At this latter locality it formed aggregations of 50-100 individuals which crowded around food items on the surface. These groups were constantly shifting and moving, with the individuals on the outside margins attempting to force their way toward the center. This same locality was also inhabited by large gyrid beetles, which were observed pursuing and apparently preying upon the *Microvelia*. At similar pools near Cinq Cases and Wilson's Well *M. diluta* was also present, but in much lower numbers, and did not exhibit the same aggregating behavior as seen at Takamaka Grove.

In addition to these freshwater localities, *M. diluta* was also found in saline habitats, being present in several limestone sinkholes behind the research station on Picard Island. These sinkholes were filled with salt water on a daily basis during the influx of the high tide, at which time the insects were observed running on the water surface. At low tide the sinkholes were devoid of water with only damp rock and sand on the bottom, and by climbing down into several of these cavities it was found that individuals of *M. diluta* simply waited on the moist sinkhole floor for the return of the tidal flow. The water in these sinkholes was clearly saline, as evidenced by the fact that chitons were inhabiting the sides of the chambers, and this tolerance for salt water may explain the wide distribution of *M. diluta* on many isolated islands in the Indian and Pacific oceans. Although several species of Microveliinae are known to inhabit mangroves in West Africa (Linnavouri, 1977), this is apparently the first record of Microveliinae from salt water habitats in the Indian Ocean (for further discussion see Polhemus, 1991).

Miyamoto (1953) provided a life history study for this species accompanied by detailed figures of all life stages.

Known distribution: Numerous authors have noted that this species is widely distributed across the Indo-Pacific region, but no paper that I have seen gives a precise definition of the range. I have examined specimens from Guam, New Guinea, Formosa, the Philippines, India, Ceylon and Aldabra. Additional literature records include Sumatra; this species is not recorded from Africa, Madagascar, or the Mascarenes, although a

subspecies is present on the Comores (see discussion above).

Material examined: ALDABRA ATOLL, **Picard:** abandoned concrete water reservoir at Aldabra Research Station, 17 March 1989, CL 8019; small tidally flooded limestone sinkhole behind Aldabra Research Station, water temp. 27° C., 10 March 1989, CL 8026; small tidally flooded sinkhole near Bassin Cabri, 17 March 1989; temporary rain pool on trail to Bassin Cabri, 20 March 1989; covered freshwater cistern at Aldabra Research Station, 20 March 1989, CL 8019. **Grande Terre:** freshwater pool near Cinq Cases, water temp. 29° C., 13 March 1989, CL 8029; pool at Wilson's Well, water temp. 29° C., 23 March 1989, CL 8038; large pool at Takamaka Grove, water temp. 32° C., 23 March 1989, CL 8039. **Malabar:** water barrel at Camp Gionnet, Anse Coco, 16 March 1989, CL 8035; water barrel at Middle Camp, nr. Passe Houareau, 19 March 1989, CL 8036; small rain pool in limestone near Middle Camp, 19 March 1989, CL 8036.

COSMOLEDO ATOLL, **Menai:** large partially uncovered freshwater cistern at Johannes Point settlement site, 27 March 1989, CL 8041; rain pools along old road near Johannes Point, 27 March 1989, CL 8041; tidally flooded limestone sinkhole near Johannes Point, 27 March 1989, CL 8041.

GERRIDAE

Limnogonus cereiventris (Signoret)

Figs. 4, 10

Gerris cereiventris Signoret 1862. Note Reunion, Ann. J: 30.

Type locality: Madagascar.

Limnogonus cereiventris Bergroth 1893. Rev. d'Ent., 12: 203.

Tenagonus cereiventris Stal 1866. Hem. Afr., 4: 262.

Gerris (*Lamprotrechus*) *leptocerus* Reuter 1883. Ofv. Finsk. Vet.-Soc. Förh., 25: 40. Type locality: Guinea. Reduced to subspecies of *cereiventris* by Poisson 1948: 99.

Gerris aegyptiaca Puton 1890. Rev. d'Ent., 9: 228. Type locality: Egypt. Syn. with *leptocerus* by Horváth 1926: 1.

Limnogonus dolosus Bergroth 1893. Rev. d'Ent., 12: 203. Type locality: Seychelles. Syn. by Kirkaldy 1899: 102.

Limnogonus aegyptiacus Bergroth 1893. Rev. d'Ent., 12: 210.

Tenagonus bottegoi Carlini 1895. Ann. Mus. Civ. Stor. Nat. Giacomo Doria, 15: 121. Type locality: Somalia. Syn. with *aegypticus* by Kirkaldy 1908: 21.

Limnogonus leptocerus Horvath 1913. J. Proc. Asia. Soc. Bengal, 9: 478.

Limnogonus cereiventris leptocerus Poisson 1948. Mem. Inst. Sci. Mad. (A), 1: 99. Syn. with *cereiventris cereiventris* by Andersen 1975: 65.

Discussion: *L. cereiventris* is a species of African affinities with a wide distribution on the islands of the western Indian Ocean. It is an easily recognizable component of the Aldabran fauna, being the only freshwater gerrid on the island, and during the present survey was seen only at several large freshwater pools on Grande Terre. This species was not encountered on Cosmoledo.

The complicated synonymy of *L. cereiventris* is treated in detail by Andersen (1975), and the synonymy listed above is nomenclatural only. The abdominal structures and details of the genitalia of both sexes were figured by Andersen (1975).

Known distribution: Africa, Madagascar, Comores, Reunion, Mauritius, Rodriguez, Seychelles (Mahe, Silhouette, Praslin, La Digue), Coetivy, Aldabra.

Material examined: ALDABRA ATOLL, **Grande Terre:** freshwater pool nr. Cinq Cases, water temp. 29° C., 13 March 1989, CL 8029; pool at Wilson's Well, water temp. 29° C., 23 March 1989, CL 8038; large pool at Takamaka Grove, water temp. 32° C., 23 March 1989, CL 8039.

MESOVELIIDAE

Mesovelina vittigera Horváth Figs. 5, 9

Mesovelina vittigera Horváth 1895. Revue d'Ent., 14: 160. Type locality: Egypt.

Mesovelina orientalis Kirkaldy 1901. Ann. Mus. Civ. Genov. (2), 20: 808. Type locality: Sumatra. Syn. by Horváth 1915: 551. Resurrected from synonymy by Horváth 1924: 135 (but interpretation not accepted by subsequent authors, eg., Andersen and Polhemus 1980: 390).

Mesovelina proxima Schouteden 1905. Ann. Soc. Ent. Belg., 69: 388. Type locality: Belgian Congo. Syn. by Horvath 1915: 551.

Discussion: A very widely distributed and adaptable species, found at Aldabra in the large freshwater pools on Grande Terre island. The coloration is usually greenish in life, fading to tan or brown after death. Individuals of this species can move across the water surface with extreme rapidity, and are often difficult to capture.

Known distribution: Widespread throughout the Eastern Hemisphere (for detailed distribution see Horváth, 1915).

Material examined: ALDABRA ATOLL, **Grande Terre:** freshwater pool nr. Cinq Cases, water temp. 29° C., 13 March 1989, CL 8029; pool at Wilson's Well, water temp. 29° C., 23 March 1989, CL 8038; large pool at Takamaka Grove, water temp. 32° C., 23 March 1989, CL 8039.

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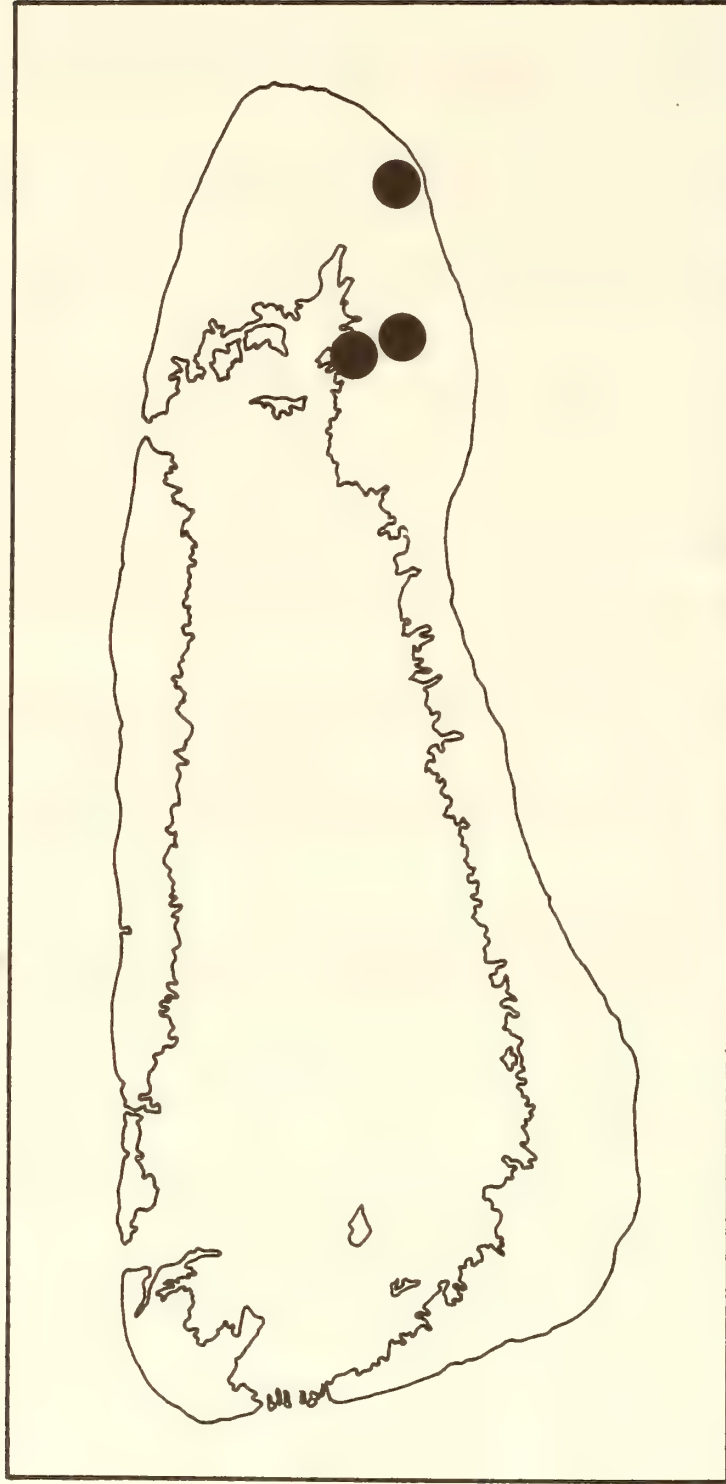


Figure 1. Distribution of *Micronecta praetermissa* on Aldabra Atoll.

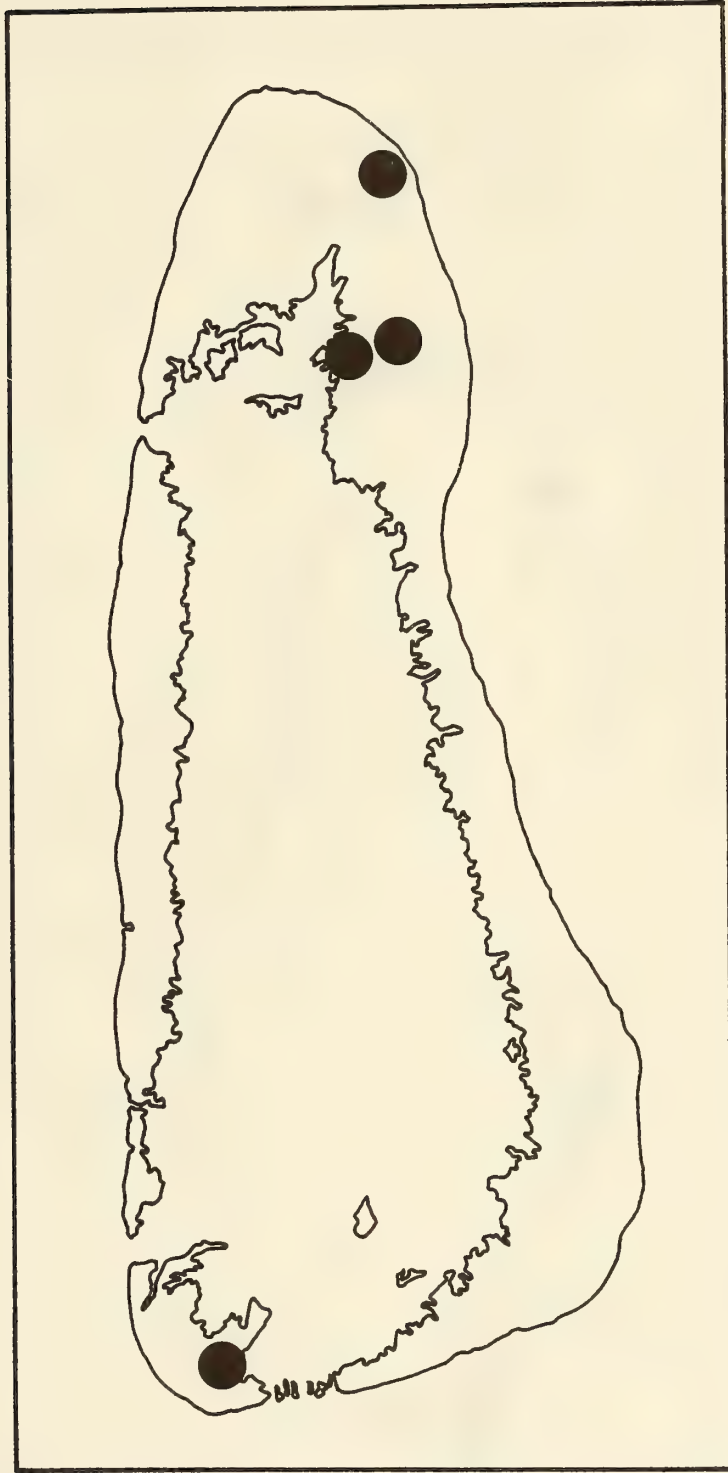


Figure 2. Distribution of *Anisops vitrea* on Aldabra Atoll.

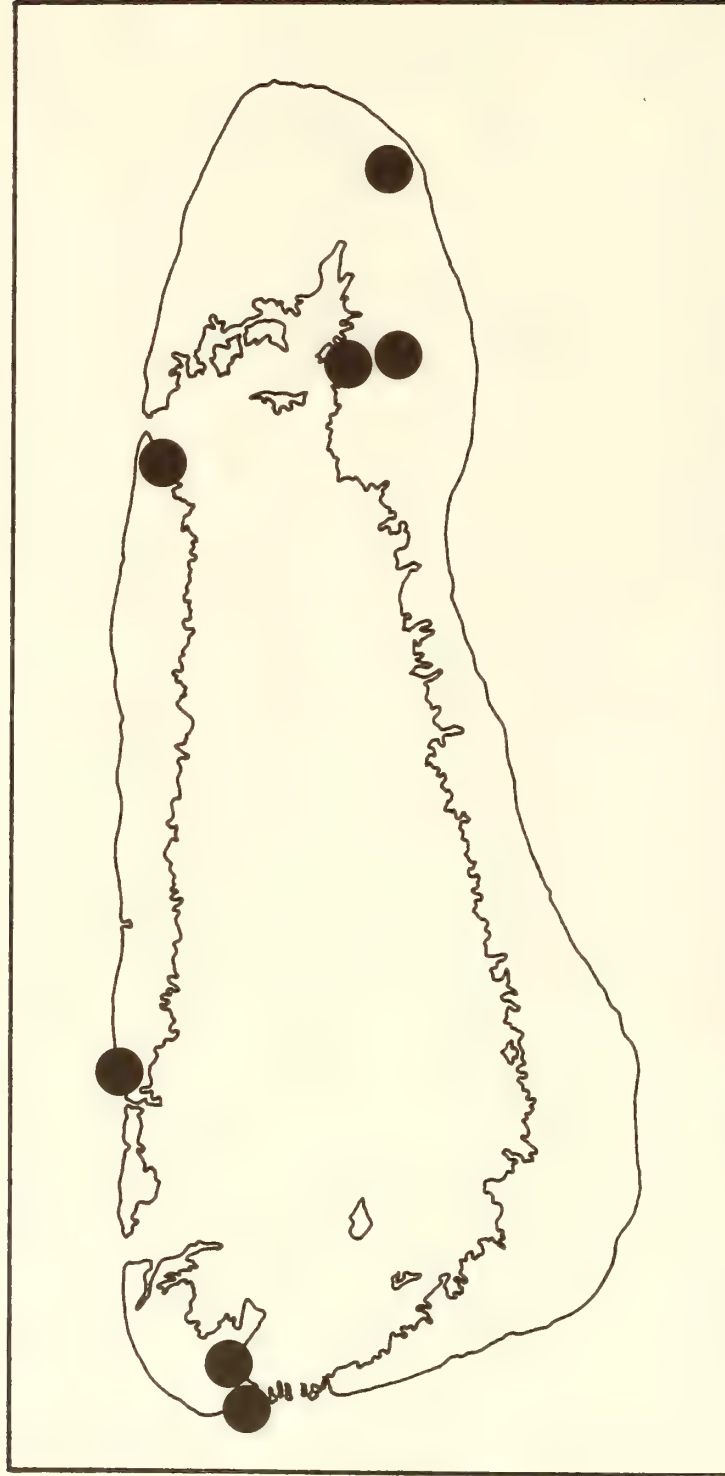


Figure 3. Distribution of *Microvelia diluta diluta* on Aldabra Atoll.

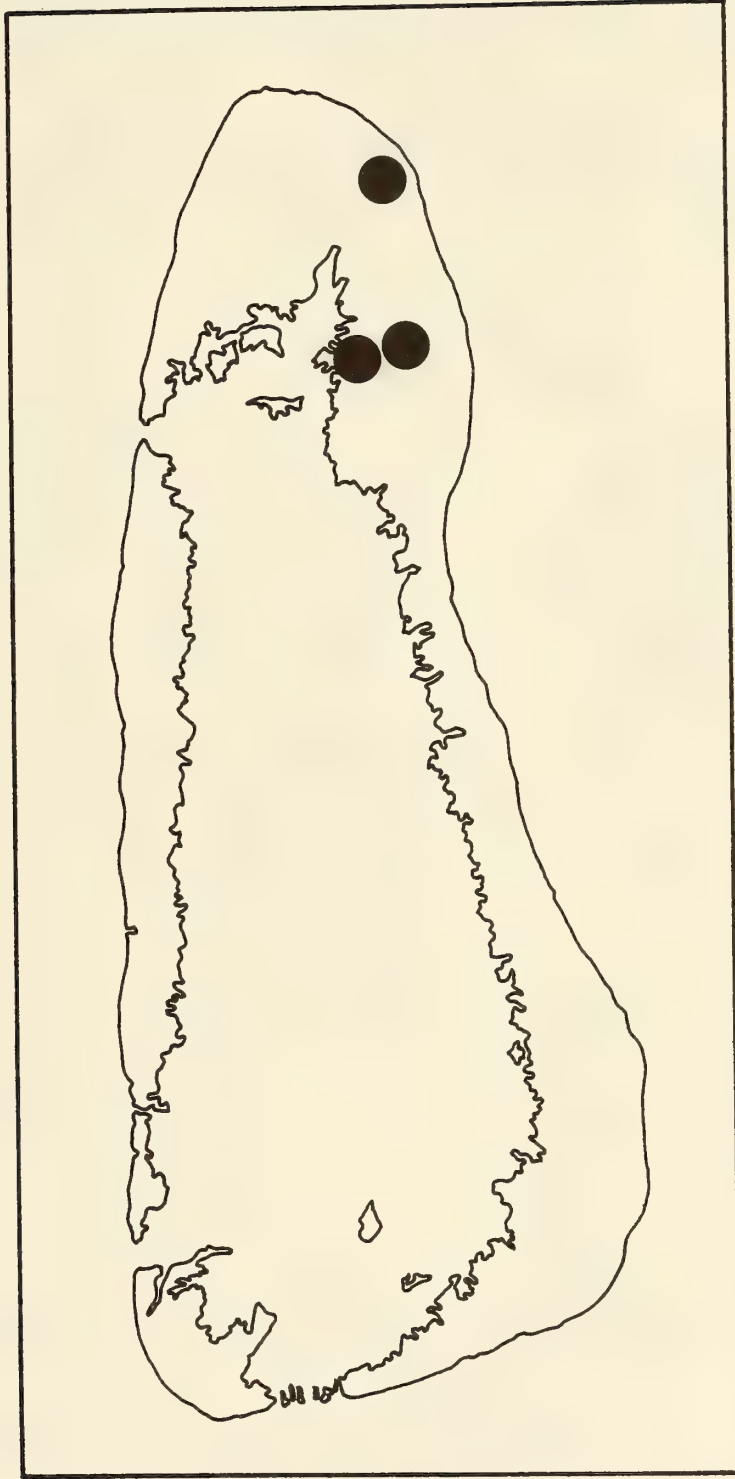


Figure 4. Distribution of *Linnogonus cereiventris* on Aldabra Atoll.

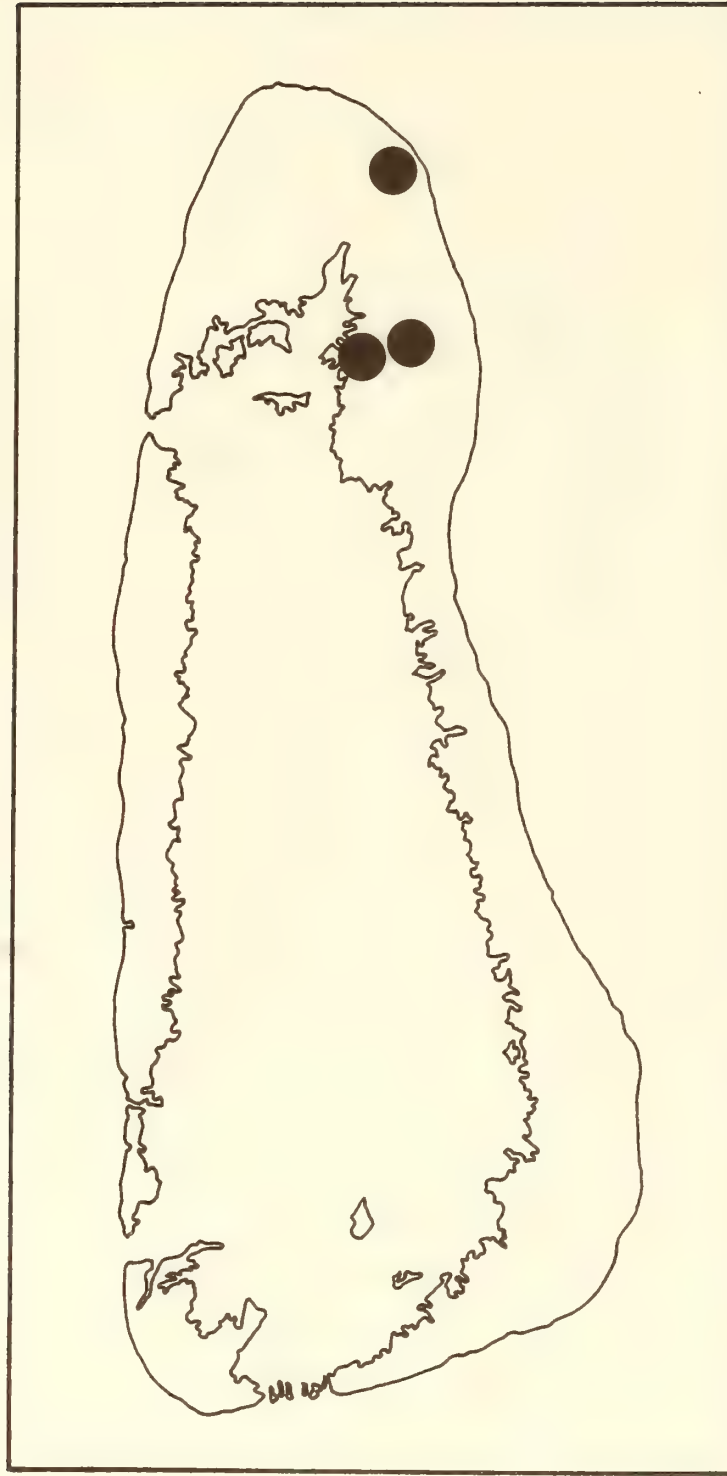


Figure 5. Distribution of *Mesovelia vittigera* on Aldabra Atoll.

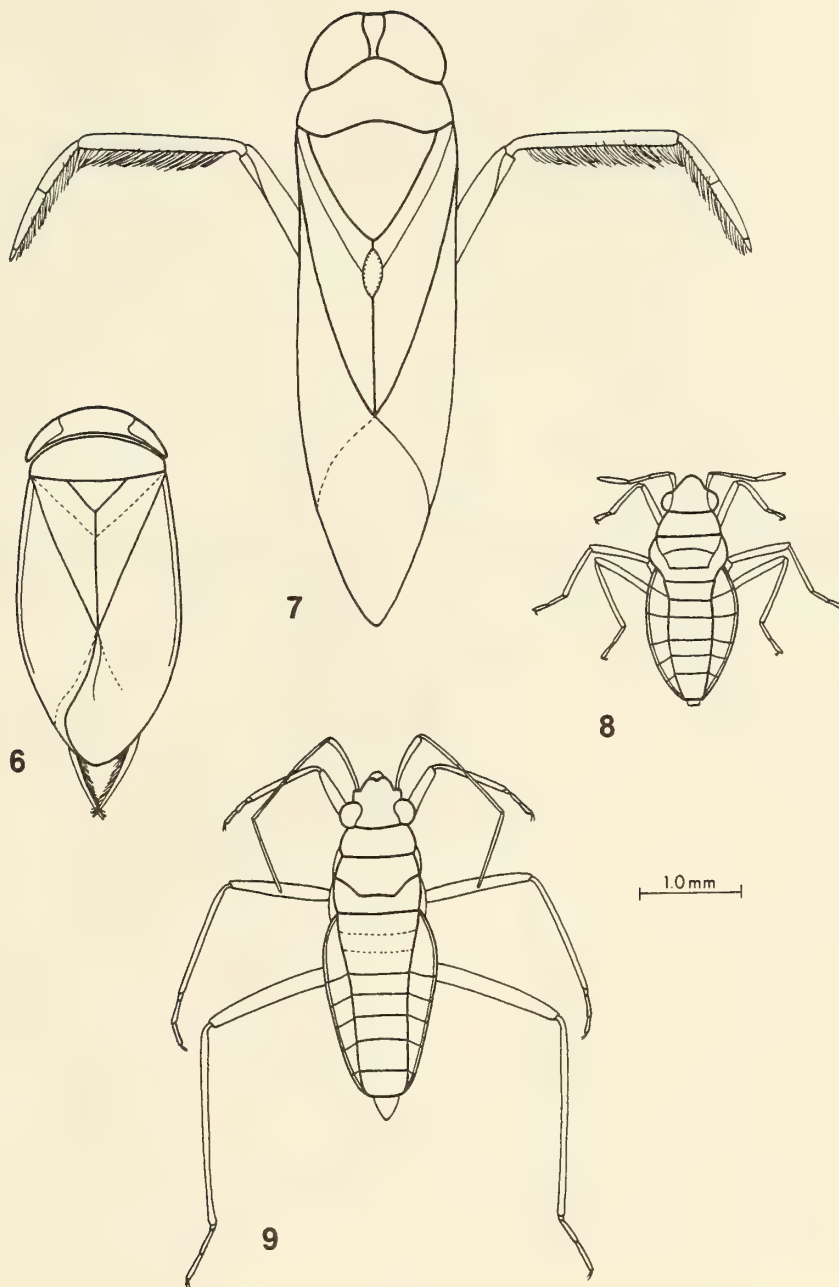


Figure 6: *Micronecta praetermissa* Poisson, dorsal habitus

Figure 7: *Anisops vitrea* Signoret, dorsal habitus

Figure 8: *Microvelia diluta diluta* Distant, dorsal habitus

Figure 9: *Mesovelia vittigera* Horváth, dorsal habitus

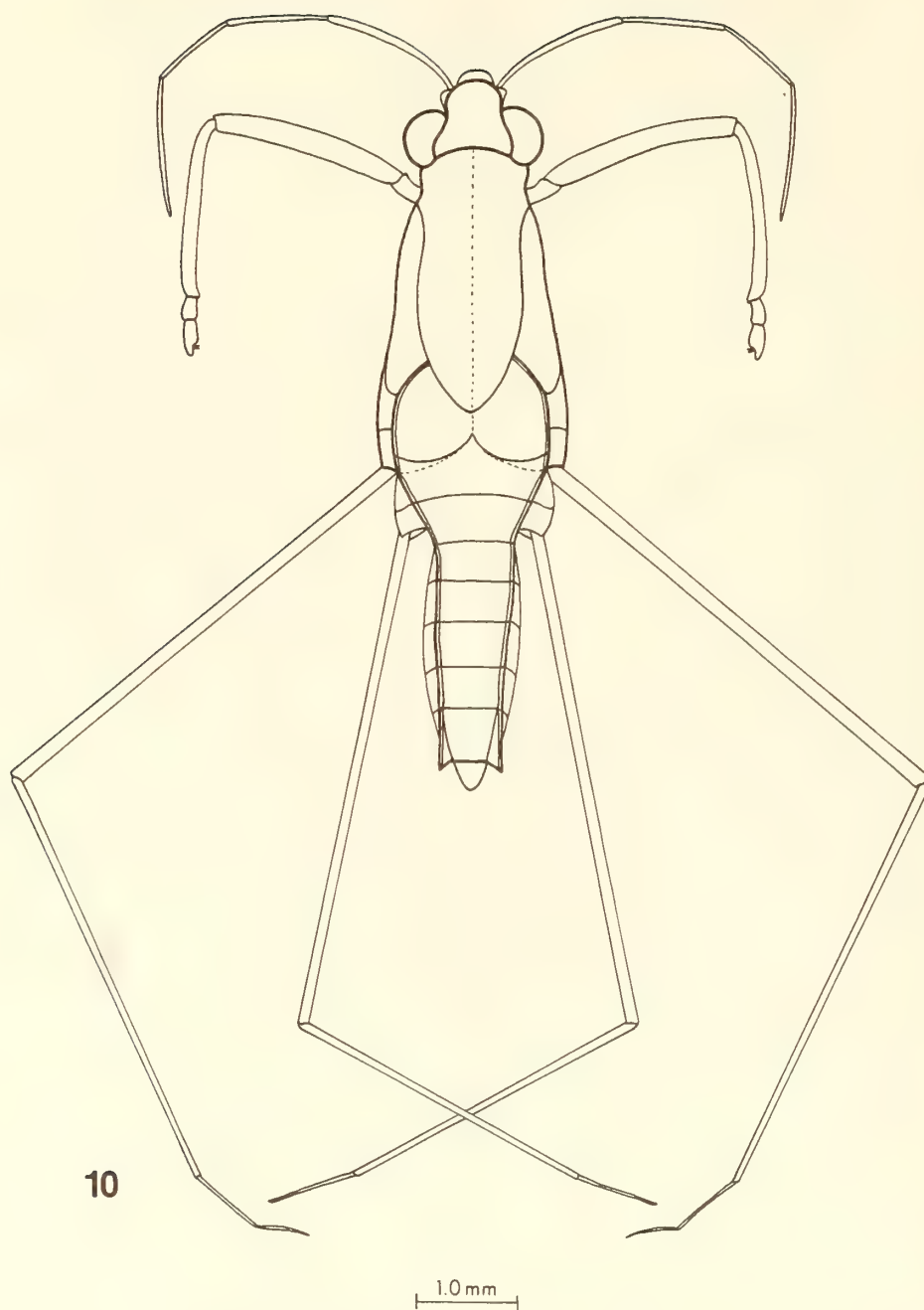


Figure 10: *Limnogonus cereiventris* (Signoret), dorsal habitus

ATOLL RESEARCH BULLETIN

NO. 382

**STUDIES ON LITTORAL AND SUBLITTORAL MACROPHYTES
AROUND THE MAURITIUS COAST**

**BY
T.G. JAGTAP**

**ISSUED BY
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STUDIES ON LITTORAL AND SUBLITTORAL MACROPHYTES AROUND THE MAURITIUS COAST

BY

T.G. JAGTAP

ABSTRACT

Floristic composition from the intertidal lagoon, reef, and subtidal (down to 20m depth) regions, around the Mauritius coast were studied to assess its present status. This provides firsthand information on the ecological distribution of mangroves, seagrasses, and subtidal marine algae. The marine flora was represented by 127 species of seaweeds, five species of seagrasses, and 3 species of mangroves.

The greatest number of species and biomass of marine algae occurred in the intertidal and the lagoonal zones. Only a few species of seaweeds, such as Asparagopsis taxiformis, Halimeda spp, Turbinaria ornata, and coralline algae, were associated with corals in the subtidal regions. The most widely distributed marine algae were Ulva spp., Enteromorpha kylini, Cladophora saviniana, Boodlea composita, Sargassum binderi, Turbinaria ornata, Gracilaria salicornia, Hypnea cornuta, Digenea simplex, and Laurencia papillosa.

The mangroves were mainly restricted to the northeast and east coasts and Rhizophora mucronata comprises almost 100% of the vegetation. The small patches of seagrasses such as Halophila ovata, Halodule uninervis, and Syringodium isoetifolium occurred commonly in patches in the lagoons towards the northeast and east.

The poor representation of marine algae and seagrasses reflects the degradation of the marine ecosystem. The steep slopes and small tidal amplitude, have resulted in the formation of fringing mangroves along the coast.

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INTRODUCTION

Marine macrophytes contribute large amounts of organic carbon in coastal waters, which enhances the overall productivity. Seaweeds are a source of agar-agar, alginate, carrageenan and pharmaceutical compounds. Detritus rich mangrove and seagrass ecosystems play an important role in stabilization of the sea bottom and in nutrient recycling. Additionally, these marine macrophytes are also utilized as food, fodder, and fertilizer on a large scale. Calcareous algae and corals form a major source of the lagoonal sediments (Mallik, 1979, Siddiquie, 1980).

Few attempts (Price, 1971; Mshigeni, 1985; Untawale and Jagtap, 1989) have been made to understand the status of marine resources along the islands of the Indian ocean region. Very limited information is available on marine floras along the Mauritius coast (Dickie, 1875; Schmitz, 1895; Boergesen, 1940-57; Mshigeni, 1985;). With a view as to the importance of island ecosystems, the survey was undertaken to study the present status of mangroves, seaweeds and seagrasses along the Mauritius coast.

DESCRIPTION OF THE STUDY AREA

Mauritius is situated in the southern tropical belt of the Indian ocean between latitudes 19°59'S and 20°32'S and longitudes 57°18'E and 57°47'E (Fig. 1). It has an area of 1865 sq km and a coastline 205 km in length. The population of Mauritius is about a million and 97% of the total population lives on Mauritius island and the rest on Rodrigues island.

TOPOGRAPHY, GEOLOGY AND GEOMORPHOLOGY

The island of Mauritius is volcanic in origin and composed of olivine basalt to doleritic basalt (Simpson, 1950). Gradual slopes and more planar habitats could be observed towards the northeast and east coasts compared to the west and south coasts of Mauritius. The reef's algal ridge is exposed to air during extreme low tide and is located as far as 4.5 km offshore along the windward east coast and very near to shore on the leeward west coast. Coral reefs are absent off seacliffs along the south and west coast. Beach rock is mainly observed towards the south coast (at Gris Gris, Ponte Aux Roches) and mudflats towards the northeast coast (Xuxville to Pointe Lascars and Trou D'Eau Douce to Mahebourg).

Towards the south, from Souille to Le Bouchon, the coast is represented by high cliffs and the beaches are formed of coral sand and gravel, basaltic gravel and boulders, and mud.

CLIMATOLOGY

Air temperatures vary seasonally from 13.5°C during May to 32.9°C during March. Mean annual rainfall is 2100 mm and ranges from 800-4000 mm (Fig. 2A). Two thirds of the rainfall occurs during summer (November-April). Relative humidity varies from 70-99%. Daily sunshine hours vary from 10.5-13.5, while solar radiation reaching the ground during the daytime ranges between 100-200 watts m^{-2} . The global solar radiation ranges from 13-21.36 MJ m^{-2} day⁻¹ and the intensity of radiation remains higher during October to March (Fig. 2B).

Mauritius is located in the southeast trade wind belt. The south and southeast coasts of Mauritius are exposed to high winds and strong waves during December to March. The mean tidal range is 0.37 m, however, it reaches 0.74 m during cyclonic conditions.

MATERIAL AND METHODS

Eighteen sites covering the entire coast were selected for algal inventory studies during September to October, 1987. However, only 10 of these were studied (Fig. 1), following preliminary observations. At site nos. 3, 4, 5, 9, and 10, transects were laid from the intertidal to subtidal regions (up to 20 m in depth) for observation and collection of biota, mainly seaweeds, mangroves, and seagrasses. Length of the transect varied from approximately 500 m at Blue Baie (St. 3) to 3000 m at Trou D'Eau Douce (St. 4) and included the reef slope, reef, forereef, lagoon and intertidal zones. The intervals between sampling points varied from 100 to 500 m -- depending upon the length of the transect. Sampling was carried out by hand picking, skin, and SCUBA diving. Intertidal zones were surveyed during low tide. Quantitative data on the few dominant species were collected in triplicate by using a 1 m^2 quadrat. Biomass was expressed as g m^{-2} on a wet weight basis.

Aerial photographs taken during 1967 were used to locate the mangrove areas along the coast. The ground truth and qualitative data were collected by visiting the mangrove sites. Quantitative data on mangroves and their

seedlings were taken in triplicate by using 10 m^{-2} and 1 m^{-2} quadrats, respectively. Specimens were preserved in 4% formalin and also mounted on herbarium sheets and have been deposited at the National Institute of Oceanography (C.S.I.R.), Goa, India.

Environmental parameters such as water temperature, salinity, pH and transparency, were measured by using a Celsius thermometer, a Sinar Salt Meter NS-3P pH meter and Secchi disk, respectively. Information on utilization of marine resources was sought by discussions with various authorities and local people.

ENVIRONMENTAL PARAMETERS

Air temperature, at the various study sites ranged from 21.4°C to 27.5°C while the water temperature ranged from 21.2°C to 28.2°C . The pH ranged between 8.3 to 8.7. Salinity of the lagoon water varied from 21.5% to 29.5%, while overlying waters in the mangrove regions, ranged from 3.5% in the upstream zone to 22.2%, along the shore. Secchi depth was observed to be 15-25 m beyond the reef, however, in the Blue Baie lagoon it was relatively low (4-5 m).

RESULTS AND DISCUSSION

During the present investigation, a total of 127 species of seaweeds (5 Cyanophyta, 34 Chlorophyta, 20 Phaeophyta and 68 Rhodophyta), 5 species of seagrasses and 3 species of mangroves were recorded, most of which were confined to intertidal and lagoonal zones (Table 1 and Fig. 3).

Seaweed species such as Ulva fasciata, U. reticulata, Enteromorpha kylini, Cladophora saviniana, Boodlea composita, Sargassum binderi, Turbinaria ornata, Gracilaria salicornia, Hypnea cornuta, Digenia simplex, and Laurencia papillosa were commonly observed along the coast. Turbinaria ornata, Asparagopsis taxiformis, and Halimeda spp. were commonly associated with coral-dominated reefs and were found in negligible quantities elsewhere. Economically important seaweed species such as Sargassum and Gracilaria were represented by 9 species each and Hypnea by 6 species. A belt of Sargassum spp. was observed at the lowest low tide mark. The highest biomass (500 wet g m^{-2}) of Sargassum was encountered at Gris-Gris, while at other sites it was negligible. Gracilaria salicornia was abundant in the rock pools and

on intertidal rocky areas. Gracilaria crassa was abundant in pool waters and from intertidal rocky areas at Gris-Gris with a biomass of 130 wet g m^{-2} . Drifted fronds of G. blodgettii, collected from the lagoon at Pointe Aux Piments might have come from deeper waters (Taylor, 1972). Though Hypnea was qualitatively rich (6 species) at Gris Gris, higher biomass (450 wet g m^{-2}) was noted at Tombeau Baie lagoon.

The intertidal expanse was generally narrow along the entire coast of Mauritius. Most of the south and southwest coast and part of west and northwest coast, was rocky and favored seaweed growth. Sandstone was common along the beaches which supported growth of Laurencia, Centroceras and Ceramium species. Most of the seaweed and seagrass species were collected in the lagoon from sand, dead coral stones, pebbles, and rocks. Though the ecological conditions such as substratum, water transparency, and irradiance were favourable, the growth of seaweeds and seagrasses was very poor. Earlier (Boergesen, 1940-57) had reported 330 species of seaweeds from Mauritius, based on collections by Dr. Vaughan, in different seasons. The poor representation of marine algae, during the present survey, could be attributed to seasonal growth and intensive grazing of algae by sea urchins (Hodgkin and Michel, 1960; Kikuchi and Peres, 1977). However, the distributional pattern of the predominant algae was similar to that observed earlier (Hodgkin and Michel, 1960). Dense populations of Colobocentrotus atratus Linne ($15-20 \text{ individuals m}^{-2}$) and Diadema spp ($4-50 \text{ individuals m}^{-2}$) were observed in the intertidal, lagoon, on the reef, and beyond, at 20 m depth.

The biomass of Ulva reticulata was estimated to be $1800 \text{ wet g m}^{-2}$ in the lagoon and $3000 \text{ wet g m}^{-2}$ at Pointe Aux Piments. However, at Tombeau Baie, Ulva spp. showed a biomass of 280 wet g m^{-2} in the lagoon. The abundances of Ulva and Enteromorpha spp. in the lagoons at Pointe Aux Piments and Tombeau Baie were correlated with organic pollutants received mostly through domestic sewage, entering in the Port Louise harbour.

Coralline algae (such as species of Jania) commonly occurred around the coast. However, species of Cheilosporum and Corallina were observed only along the south coast at Pointe Aux Roches and Gris-Gris. The encrusting coralline outer ridge appeared towards the seaward side, similar to the islands in Indo-Pacific regions (Womersley and Bailey, 1969; Littler and Doty, 1975; Jagtap, 1987). The species like Lithophyllum and

Lithothamnion have been reported (Boergesen, 1940-57; Hodgkin and Michel, 1960) to be common encrusting forms.

Small patches of seagrass beds of Halophila ovata, Halodule uninervis, and Syringodium isoetifolium were common at depths of 1-4 m in the lagoon. Halophila stipulaceae and Thalassodendron ciliatum were rarely distributed in the lagoons along the east coast. Marine algae such as Enteromorpha clathrata, Lyngbya majuscula, Phomidium sp., Oscillatoria spp., Calothrix contarenii, and Melobesia sp. were commonly associated with seagrass beds. Cyanophyta, associated with the seagrass ecosystem, serve as food for reef fishes and also enrich the environment by nitrogen fixing (Dawson et al., 1955). Calothrix contarenii has been reported from the coral environments of India (Iyengar and Desikachary, 1944).

The total mangrove cover along the Mauritius coast was estimated to be about 20 km². The mangrove flora, comprised mainly of Rhizophora mucronata, was restricted to the northeast and east coasts of Mauritius (Fig. 1). Few patches of young R. mucronata were observed towards the southeast and southwest coasts at Bel Ombre and Baie Du Cap. Occasional plants of Bruguiera gymnorhiza were observed in the upstream brackish water regions of Pointe Lafayette, Trou D'Eau Douce and Ferney and Mahebourg. Acrostichum aureum was common in the upstream regions highly influenced by freshwater. Other oceanic islands closer to Mauritius have been reported to have more number of species (Untawale and Jagtap, 1989). However, almost 100% of the mangrove area along the Mauritius coast was dominated by R. mucronata, which could be attributed to its successful colonization and competitive advantage over new prospective colonizers. The height of the Rhizophora strands varied from 2-7 m and the density ranged from 0.7-1.5 trees m⁻². The seedling density was observed to be very high (20-30 individuals m⁻²). Total mangrove cover along the Mauritius coast was estimated to be about 20 km². The substratum of mangrove regions was sandy gravel, sandy clay and silty clay with pebbles and rock crevices. Relatively more rainfall, gradual slopes and protection from southeast trade winds result in more freshwater input and siltation along the northeast and east coasts of Mauritius (Fig. 2A). The occurrence of mangroves mainly along the northeast and east coasts may be attributed to more freshwater influence, more siltation due to protection of the coast, and higher humidity. Topographical features and tidal height have restricted the distribution of seedlings resulting in fringing mangroves.

Large mangrove areas were utilized by earlier settlers, mainly for fuel and are presently being reclaimed for civil development. Some of the mangrove areas have been privately utilized for farming of mullet, crab, shrimp, and seacarp. The mangrove area at Trou D'eau Douce, has been utilized for recreational purposes. Mangrove resources of Mauritius, though limited, are of great significance in protecting the shoreline during cyclonic conditions. Therefore, it is necessary to develop management policies for conservation and utilization of mangroves in Mauritius.

Dynamite fishing, overexploitation of reefs and lagoons for coral and sand (for commercial sale as souvenirs, lime production, and construction material) were commonly exercised. Lagoons are also being utilized for dumping effluents from sugar refineries and domestic sewage. Presently about 800 metric tons of coral stones and 1000-1500 tons of sand are being extracted every year from the coral environments of Mauritius (Mr. Chauveau, personal communication) for lime production. The lime production in Mauritius started during 1962, and since then, coral environments have been exploited on a large scale.

SUMMARY

The present observations indicate that Mauritius seaweeds are not abundant; however, there seems to be a great potential for economically important species such as Gracilaria, Hypnea, and Sargassum. Eucheuma species, reported (Mschigeni, 1985) from Pointe Aux Roches and from Rodrigues island of Mauritius, could be cultivated around Mauritius. Turbinaria ornata, Asparagopsis taxiformis, and Halimeda spp. form a characteristic flora in association with coral reef environments, similar to other coral environments from the Indian ocean (Jagtap, 1987; Untawale and Jagtap, 1988). An intense growth of Ulva spp. and Enteromorpha spp. in Baie de Tombeau and Pointe Aux Piments correlates with a heavy influence of organic and domestic pollution. The seagrass beds from the lagoon have been reduced to a large extent by the continuous sand removal process. The mangroves, mainly Rhizophora mucronata, occur along northeast and east coasts of Mauritius. Dynamite fishing and overexploitation of corals and sand for commercial purposes is causing severe damage to the entire coral reef, lagoons, and their associated biotas.

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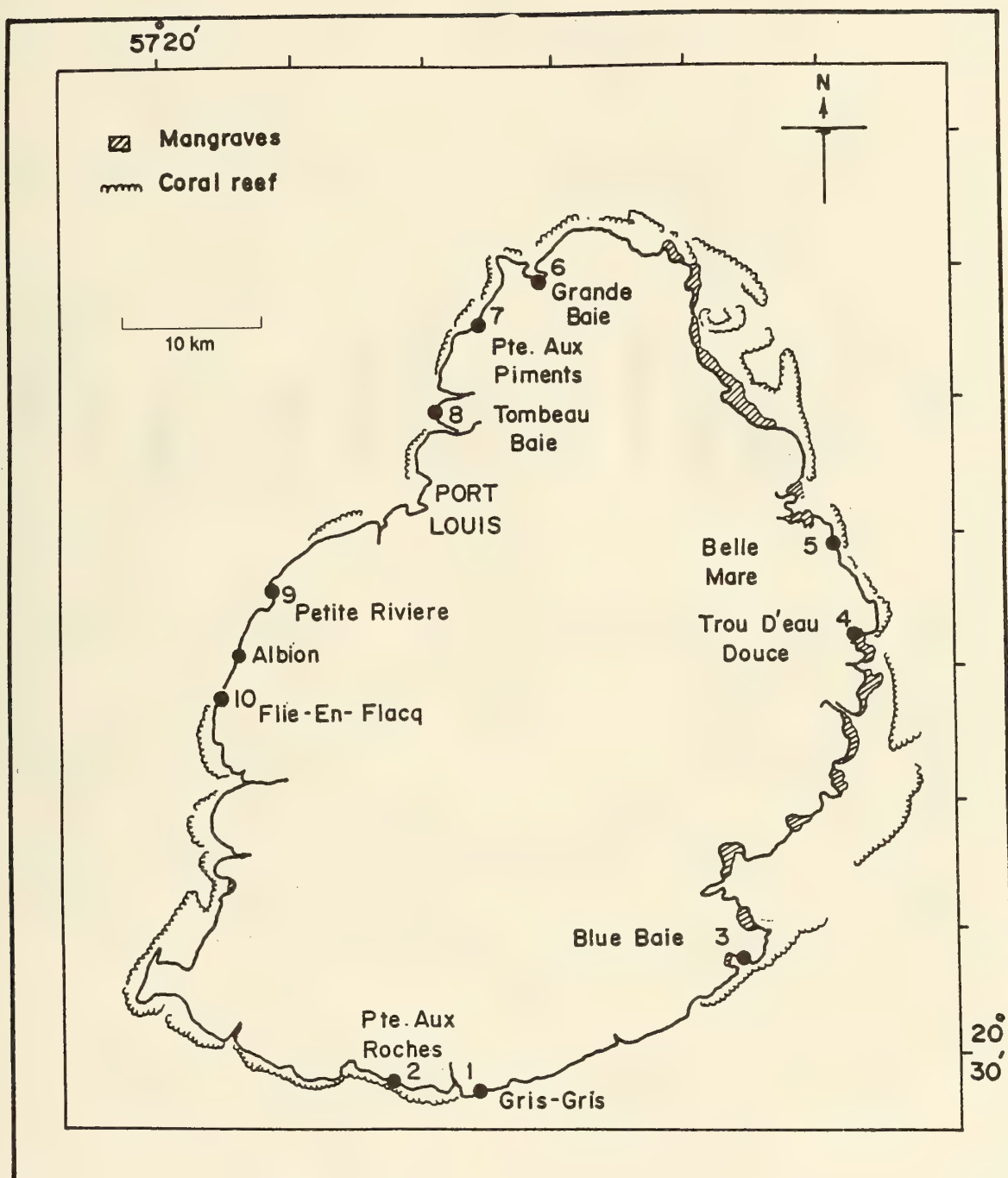


Fig. 1 Index map of Mauritius showing distribution of coral reefs and mangroves. Numbers indicate sample sites.

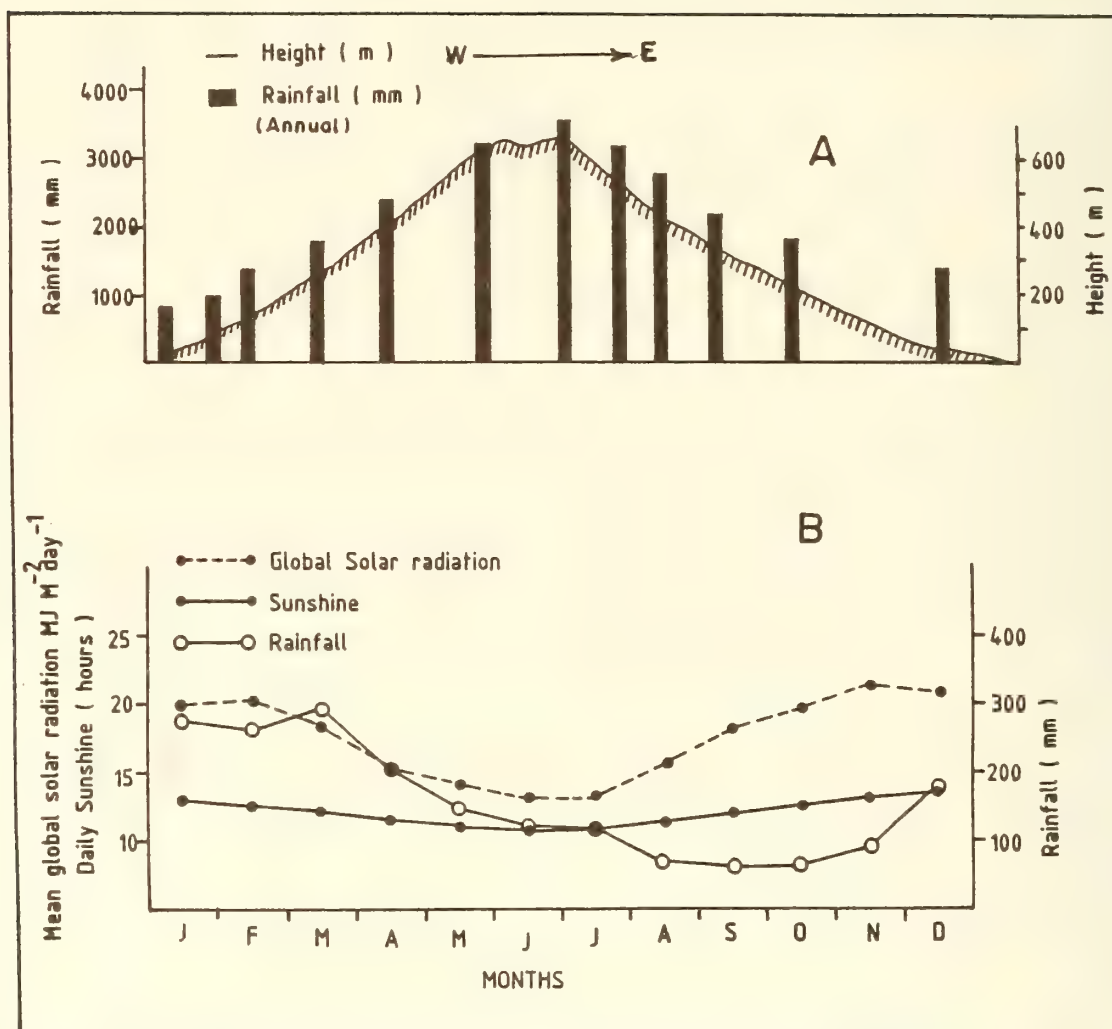


Fig. 2 Topography and climatological data of Mauritius.



LEGENDS

	<u>Ulva fasciata</u>		<u>Gracilaria edulis</u>
	<u>U. pertusa</u>		<u>G. spinuligera</u>
	<u>U. reticulata</u>		<u>G. salicornia</u>
	<u>Enteromorpha</u> spp.		<u>G. crassa</u>
	<u>Chaetomorpha antennina</u>		<u>Ceratodictyon spongiosum</u>
	<u>Halimeda</u> spp.		<u>Hypnea</u> spp.
	<u>Boodlea composita</u>		<u>Centroceros clavulatum</u>
	<u>Dictyosphaeria cavernosa</u>		<u>Digena simplex</u>
	<u>Ectocarpus</u> spp.		<u>Acanthophora spicifera</u>
	<u>Colpomenia sinuosa</u>		<u>Laurencia papillosa</u>
	<u>Padina gymnospora</u>		<u>Halophila stipulaceae</u>
	<u>Chnoospora implexa</u>		<u>H. ovalis</u>
	<u>Sargassum</u> spp.		<u>Thalassodendron ciliatum</u>
	<u>Turbinaria ornata</u>		<u>Halodule uninervis</u>
	<u>Asparogopsis taxiformis</u>		<u>Syringodium isoetifolium</u>
	<u>Gelidiella acerosa</u>		<u>Ipomea Pes-Capre</u>
	<u>Amphiroa</u> spp.		Mangroves
	<u>Cheilosporum</u> spp.		<u>Acropora</u> spp.
			Alcyonaceans.

Fig. 3. Profiles (A-F) at various localities, depicting distribution of major biota, along the Mauritius coast (A - Gris-Gris, B - Point Aux Roches, C - Petite Rivere, D - Flic-En-Flacq, E - Belle Mare, F - Trou D'Eau Douce).

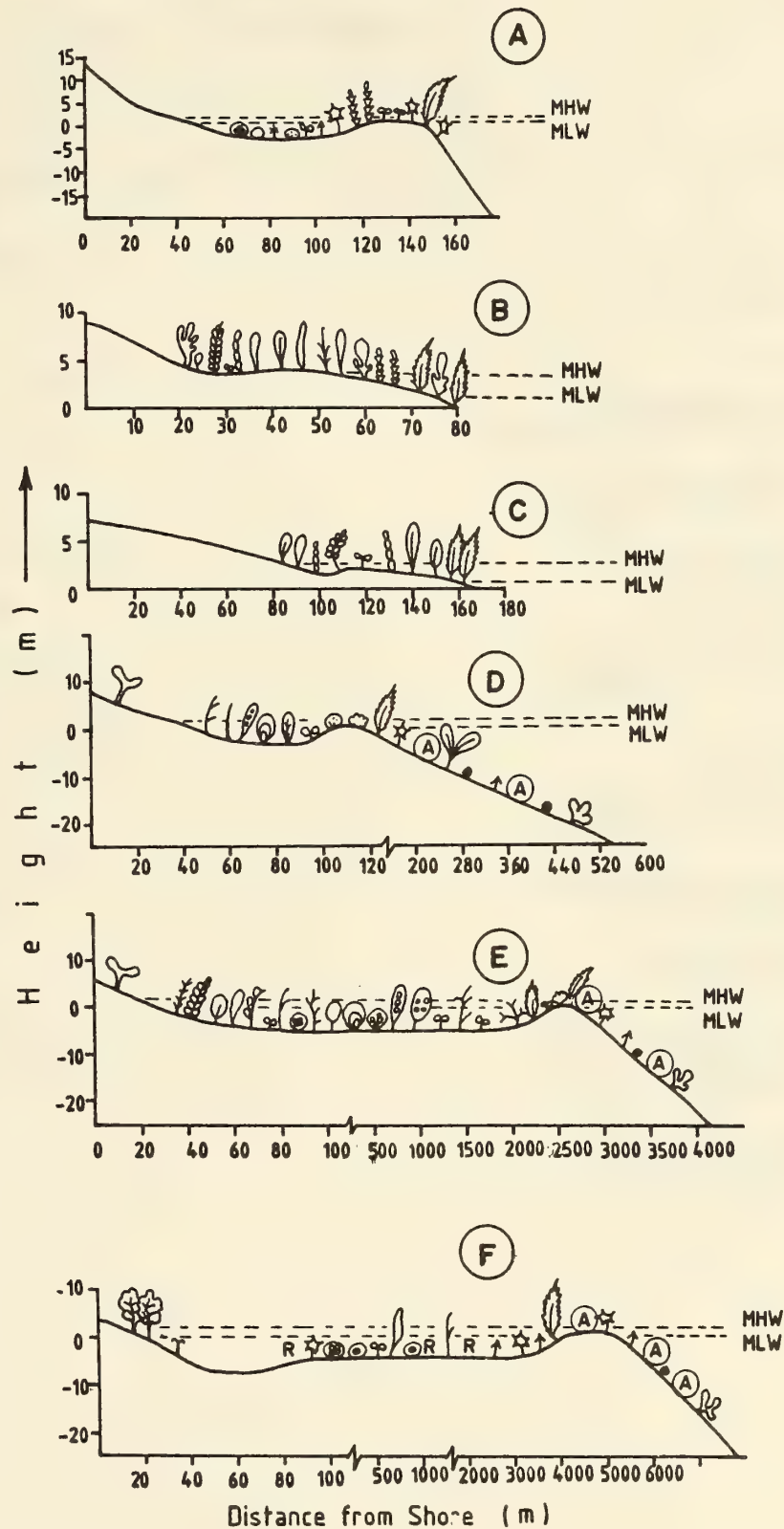


Table I
MARINE FLORA OF MAURITIUS
(collected during Sept.-Oct. , 1987) 1

Stations	South coast			East coast		North east coast		West coast		
	1	2	3	4	5	6	7	8	9	10
Name of Species										
Marine algae										
Cyanophyta										
<u>Calothrix contarenii</u> (Zanardo) Bornet & Flahaut										+
<u>Lyngbya majuscula</u> Harv. ex. Gomont				+	+					+
<u>Oscillatoria</u> sp.									+	
<u>O. sancta</u> Kutz.				+						
<u>Phormidium crosbyanum</u> Tilden							+			
Chlorophyta										
<u>Avrainvillea gracillima</u> Boerges.					+					
<u>Boergensenia forebesii</u> (Harv.) Feldm.	+	+	+							
<u>Boodlea composita</u> (Harv.) Brand	+	+			+		+			+
<u>Bryopsis pennata</u> Lamour. var. <u>secunda</u> (Harv.) Collins & Harv.		+								+
<u>Caulerpa occidentalis</u> (J. Ag.) Jaasund	+		+							

	1	2	3	4	5	6	7	8	9	10
<u>C. racemosa</u> (Forssk.) Weber-van Bosse var. <u>clavifera</u> (Turn.) Weber-van Bosse		+								
<u>C. taxifolia</u> (Vahl) C. Ag.							+			
<u>Chaetomorpha antennina</u> (Bory) Kutz.		+								
<u>C. linoides</u> (Ag.) Kutz.							+			
<u>C. natalensis</u> (Hering) De Toni		+								
<u>C. patentiramea</u> (Mont.) Kutz.					+				+	
<u>C. vagabunda</u> (L.) Van den Hoek										+
<u>C. vaughani</u> Boerges.				+						
<u>Cladophora saviniana</u> Boerges.	+		+		+	+	+	+		
<u>C. sundanensis</u> Reinbold	+									
<u>Cladophoropsis</u> sp.										+
<u>Codium arabicum</u> Kutz.					+					
<u>C. geppii</u> Schmid.				+	+					
<u>Dictyosphaeria cavernosa</u> (Forssk.) Boerges.	+	+			+					
<u>Enteromorpha</u> sp.	+						+	+		
<u>E. clathrata</u> (Roth) J. Ag.	+		+							+
<u>E. compressa</u> (L.) Grev.			+					+		
<u>E. flexuosa</u> sp. <u>linziformis</u> Bliding							+			

	1	2	3	4	5	6	7	8	9	10
<u>E. kylini</u> Bliding Sensu Dawson	+				+	+		+		+
<u>E. linza</u> (L.) J. Ag.								+		
<u>Halimeda opuntia</u> (L.) Lamour.			+		+					
<u>H. tuna</u> (Ellis & Sol.) Lamour.	+			+	+					
<u>Microdictyon</u> sp.		+								
<u>Rhizoclonium kernerii</u> Stockm.	+									
<u>Ulva fasciata</u> Dellile	+	+	+	+	+		+		+	
<u>U. pertusa</u> Kjell.							+	+		
<u>U. reticulata</u> Forssk.		+		+	+		+	+		
<u>Valonia aegagropila</u> C. Ag.						+		+		
Phaeophyta										
<u>Chnoospora implexa</u> (Hering) J. Ag.				+			+			
<u>Colpomenia sinuosa</u> (Derb. & Sol.)	+	+	+	+	+	+	+	+	+	+
<u>Dictyopteris delicatula</u> Lamour.					+					+
<u>Dictyota bartayresii</u> Lamour. Sensu Vick.	+	+		+						+
<u>D. cervicornis</u> Kutz.				+			+			
<u>Ectocarpus indicus</u> Sonder	+						+			
<u>E. mitchellae</u> Harv.		+	+						+	
<u>Hydroclathrus clathratus</u> (Bory) Howe					+					

	1	2	3	4	5	6	7	8	9	10
<u>Lobophora variegata</u> (Lamx.) Womersley	+	+		+	+	+	+		+	+
<u>Padina gymnospora</u> (Kutz.) Sonder	+	+				+		+		
<u>Sargassum</u> sp. 1	+									
<u>Sargassum</u> sp. 2	+									
<u>S. aquifolium</u> (Turn.) J. Ag.										+
<u>S. binderi</u> Sonder	+	+		+	+					+
<u>S. densifolium</u> Zan.					+					
<u>S. duplicatum</u> J. Ag.	+	+	+	+					+	
<u>S. paniculatum</u> J. Ag.		+								
<u>S. polycystum</u> C. Ag.		+				+				
<u>S. porterinum</u> Zan.	+	+					+			
<u>Turbinaria ornata</u> (Turn.) J. Ag.	+	+	+	+	+	+	+			
Rhodophyta										
<u>Acanthophora spicifera</u> (Vahl.) Boerges.		+		+				+		
<u>Agardhiella tenera</u> (J. Ag.) Schmitz								+		
<u>Ahnfeltia</u> sp.	+			+						
<u>Amphiroa anastomosans</u> Weber-van Bosse										+
<u>A. fragilissima</u> (L.) Lamour.	+									
<u>A. rigida</u> Lamour.	+			+			+			

	1	2	3	4	5	6	7	8	9	10
<u>Asparagopsis taxiformis</u> (Delile) Coll. & Harv.					+					
<u>Callymenia morelii</u> (Mont. & Mill.) Boerges.		+								
<u>Caloglossa leprieurii</u> (Mont.) J. Ag.				+						
<u>Centroceros clavulatum</u> (C. Ag.) Mont.	+	+	+	+	+	+	+	+	+	+
<u>Ceramium camouii</u> Dawson	+									
<u>Ceratodictyon spongiosum</u> Zan.				+						
<u>Champia parvula</u> (C. Ag.) Harv.				+						
<u>Cheilosporum acutilobum</u> Aresch. (Decasne)		+								
<u>C. jungermannioides</u> Rupr.	+									
<u>Coelothrix</u> sp.	+									
<u>Corallina subulata</u> Ellis & Sol.	+									
<u>C. polydactyla</u> Mont. & Mill.		+								
<u>Dasya pedicellata</u> (C. Ag.) C. Ag.				+						
<u>Desmia pulvinata</u> J. Ag.							+			
<u>Digenea simplex</u> (Wulf.) C. Ag.	+	+			+	+	+	+	+	+
<u>Galaxuara marginata</u> Lamour.		+								
<u>G. oblongata</u> (Ellis & Sol.) Lamour.		+		+						

	1	2	3	4	5	6	7	8	9	10
<u>G. obtusa</u> (Ellis & Sol.) Lamour.										+
<u>G. rugosa</u> (Lol.) Lamour.		+								
<u>G. subverticillata</u> Kjell.		+								
<u>Gelidium</u> sp.										+
<u>G. crinale</u> (Turn.) Lamour.							+	+		
<u>Gelidiella acerosa</u> (Forssk.) Feldm. & Hamel.	+			+				+		
<u>G. myrioclada</u> (Boerges.) Feldm. & Hamel.								+		
<u>Gelidiopsis scoparia</u> (Mont. & Mill.) Schmitz								+		
<u>Gracilaria</u> sp.		+								
<u>G. arcuata</u> Zan.				+			+			
<u>G. blodgettii</u> (Harv.)							+			
<u>G. crassa</u> Harv.	+	+						+		
<u>G. dura</u> (Ag.) J. Ag.								+		
<u>G. edulis</u> (J. Ag.) Silva							+			
<u>G. Millardetii</u> (Mont.) J. Ag.	+							+		
<u>G. salicornia</u> J. Ag.	+	+		+	+	+	+	+	+	+
<u>G. spinuligera</u> Boerges.			+					+		

	1	2	3	4	5	6	7	8	9	10
<u>Gymnogongrus</u> sp.		+								
<u>Halymenia</u> <u>maculata</u> J. Ag.								+		
<u>Hypnea</u> sp				+						
<u>H. charoides</u> Lamour.	+			+					+	
<u>H. cornuta</u> (Lamour.) J. Ag.	+	+		+	+		+	+	+	+
<u>H. musciformes</u> (Wulfen) Lamour.	+	+								
<u>H. nidulans</u> Setch.			+							
<u>H. pannosa</u> J. Ag.	+	+								
<u>H. valentiae</u> (Turn.) Mont.				+						
<u>Jania</u> <u>adhaerens</u> Lamour.	+	+	+	+	+	+	+	+	+	+
<u>J. pumila</u> Lamour.	+									
<u>Laurencia</u> <u>fexilis</u> Setch.	+									
<u>L. papillosa</u> (Forssk.) Grev.	+	+	+		+		+		+	
<u>Liagora</u> <u>jadini</u> Boerges.										+
<u>L. valida</u> (Harv.)					+					
<u>Lithothamnion</u> sp.				+						
<u>Melobesia</u> sp.	+		+		+					
<u>Polysiphonia</u> <u>gorgoniae</u> Harv.				+						
<u>P. platicarpa</u> Boerges.				+						+
<u>Pseudogloiophloea</u> sp.					+					

	1	2	3	4	5	6	7	8	9	10
<u>Pterocladia nana</u> Ckamura							+			
<u>P. pinnata</u> (Hud.) Papenf.	+									
<u>Rhodymenia</u> sp.					+					
<u>Sarcodia</u> sp.		+								
<u>S. montagneana</u> J. Ag.	+							+		
<u>Sarconema filiforme</u> (Sond.) Kylin	+	+								
<u>Soliera tenuis</u> Zhang & Xia									+	
<u>Wurdmannia</u> sp. ?							+			
Seagrasses										
<u>Halodule uninervis</u> (Forssk.) Aschers	+	?	+	+						
<u>Halophila ovata</u> (Gaud.)			+	+	+					
<u>H. stipulcea</u> (Forssk.) Aschers				+	+					
<u>Syringodium isoetifolium</u> (Aschers) Dandy	+	?		+			+			
<u>Thalassodendron ciliatum</u> (Forssk.) Den Hartog				+						
Mangroves										
<u>Acrostichum aureum</u> L		Rare								
<u>Bruguiera gymnorhiza</u> (L.) Lamk.		Stray			Only few plants upstream backwaters along Northeast coast					
<u>Rhizophora mucronata</u> Lamk.		Dominant			100%					

ATOLL RESEARCH BULLETIN

NO. 383

**STUDIES ON THE BIOLOGY AND ECOLOGY OF
THE INTERTIDAL ANIMALS OF CHICHIJIMA ISLAND IN THE
OGASAWARA (BONIN) ISLANDS**

I. LIST OF COLLECTED SPECIES WITH COMMENTS ON SOME SPECIES

BY

AKIRA ASAKURA, SHIROOU NISHIHAMA, AND YASUO KONDO

**ISSUED BY
NATIONAL MUSEUM OF NATURAL HISTORY
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AKIRA ASAKURA*, SHIROU NISHIHAMA**, AND YASUO KONDO***

INTRODUCTION

The Ogasawara (Bonin) Islands are subtropical, oceanic islands, located in the north west Pacific (Lat. 27° N, Long. 142° E). The nearest landmass is the Japan Islands situated ca. 1000 km to the north (Fig. 1). Many endemic species have been found in its terrestrial (Ono & Masuda, 1981; Ono & Sugawara, 1981; Kobayashi, 1978; Habe, 1969; Habe *et al.*, 1978) and marine environments (Okutani, 1986; Shigei, 1970; Hirohito, 1974; Habe *et al.*, 1978; Imajima 1970; Sugano, 1973; Ooishi, 1970; Kurata *et al.*, 1975).

The authors visited Chichijima Island of the Ogasawara Islands three times, in April 1986, May 1989, and June 1990. The purpose of the visits was to study the biological and ecological aspects of the intertidal animals there, which have received little attention to date.

In this paper, a list of species collected through those trips is presented, which includes one new species of a hermit crab, *Pagurus insulae* in Asakura (1991a), two new subspecies of gastropods, *Notoacmea schrenckii boninensis* in Asakura & Nishihama (1987a) and *Monodonta perplexa boninensis* in Asakura & Nishihama (1987b), and one new record of a hermit crab, *Calcinus guamensis* Wooster, from Japan (Asakura, 1991b).

PREVIOUS WORK

Four main marine biological surveys of the Ogasawara Islands have been conducted; 1. Toba Aquarium [June to July 1968](Toba Aq. & Asahi. Publ., 1970), 2. the Ministry of Education [summer of 1968](Shigei, 1970), 3. Officials from the Ministry of Health and Welfare and the Tokyo Metropolitan government [November to December 1968](Imajima, 1970), and 4. National Science Museum [1975 to 1976](Habe *et al.*, 1978). Several other works, in particular taxonomic works, are well documented in Habe *et al.*, (1978), Ooishi (1970), Takeda & Miyake (1976), and Eldredge (1975).

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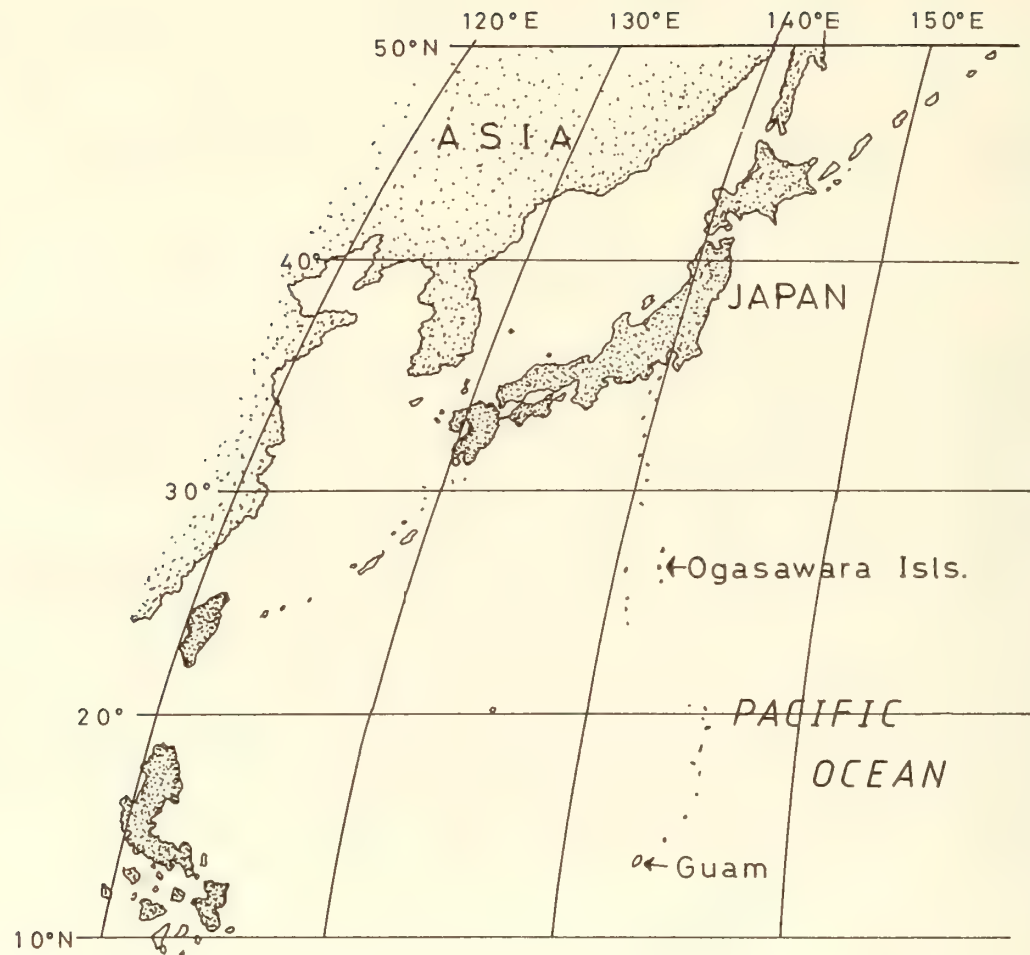


Fig. 1. Location of the Ogasawara Islands.

P R E S E N T W O R K

Judging from the photographs of the Chichijima island taken in 1968 (in Toba Aq. and Asahi. Publ., 1970), the landscape has changed drastically. In particular, the west coast has recently been rapidly developed. The natural coastal zones in the inner part of Futami Bay (the largest bay in the island) have also been damaged in order to construct a larger harbor with concrete-protected shore lines, and some species of intertidal invertebrates were exterminated (Asakura & Nishihama, 1988).

In our investigations, we quantitatively sampled many invertebrates from whole coastal areas of Chichijima. Since the destruction of those coastal areas continues, this sample will have the value of recording for posterity the animals that inhabited this region. Many rare and endemic species inhabit the islands, and we feel that the conservation of these coastal areas is important.

L O C A T I O N O F S A M P L I N G P O I N T S

All sampling points were located in the intertidal zones of rocky shores on the coast of Chichijima Island (Fig. 2). Detailed descriptions of topography of each site have been already published in Asakura & Nishihama (1987a,b; 1988) and Asakura *et al.* (1991). Collections were made at low tide during the spring tide. Samples were preserved in 10% formalin solution, brought to the laboratory and identified to species.

Following references were used for identification; Mollusca (Okutani, 1986; Habe & Okutani, 1975), Crustacea (Miyake, 1982, 1983), Annelida (Utinomi, 1975), and Echinodermata (Utinomi, 1975). Unidentified species were sent to an authority for each taxon, and these identifications were followed.

ACKNOWLEDGEMENTS ----- We wish express our heartfelt thanks to the following persons for identifying specimens and contributing valuable information: Dr. T. Habe, President of the Malacological Society of Japan (Mollusca), Dr. S. Miyake, President of the Carcinological Society of Japan (Crustacea, Anomura), Dr. K. Sakai, Professor of Shikoku Women's University (Crustacea, Anomura), Dr. K. Baba, Professor of Kumamoto University (Crustacea, Anomura), Dr. Y. Miya, Professor of Nagasaki University (Crustacea, Macrura), Dr. M. Takeda, National Science Museum (Crustacea, Brachyura), Dr. T. Yamaguchi, Associate Professor of Chiba University (Crustacea, Cirripedia). We also express our sincere appreciation to Professor T. Yanagisawa, the Ogasawara Research Committee of Tokyo Metropolitan University, Mr. K. Nishimura, the Ogasawara Fishery Center, Mr. Y. Kurata, the Ogasawara Marine Center, Mr. Y. Matsumoto, Toba Aquarium, and Dr. B.D. Smith, Guam University Marine Laboratory, for their valuable suggestions, advises, and aid in the bibliographical survey. Thanks are also due to Mr. T. Kurozumi, Natural History Museum and Institute, Chiba and an anonymous reviewer for useful comment on the manuscript. Staffs of the Ogasawara Youth Hostel and T. Nakajima, the Urayasu Official, kindly assisted us in our field works. This work is a part of results of the special project on the "Investigation of the Nature of the Boso, Izu, Ogasawara, and Mariana Archipelagos", financially supported by the grant of the Natural History Museum and Institute, Chiba from the Educational Department of Chiba Prefecture.

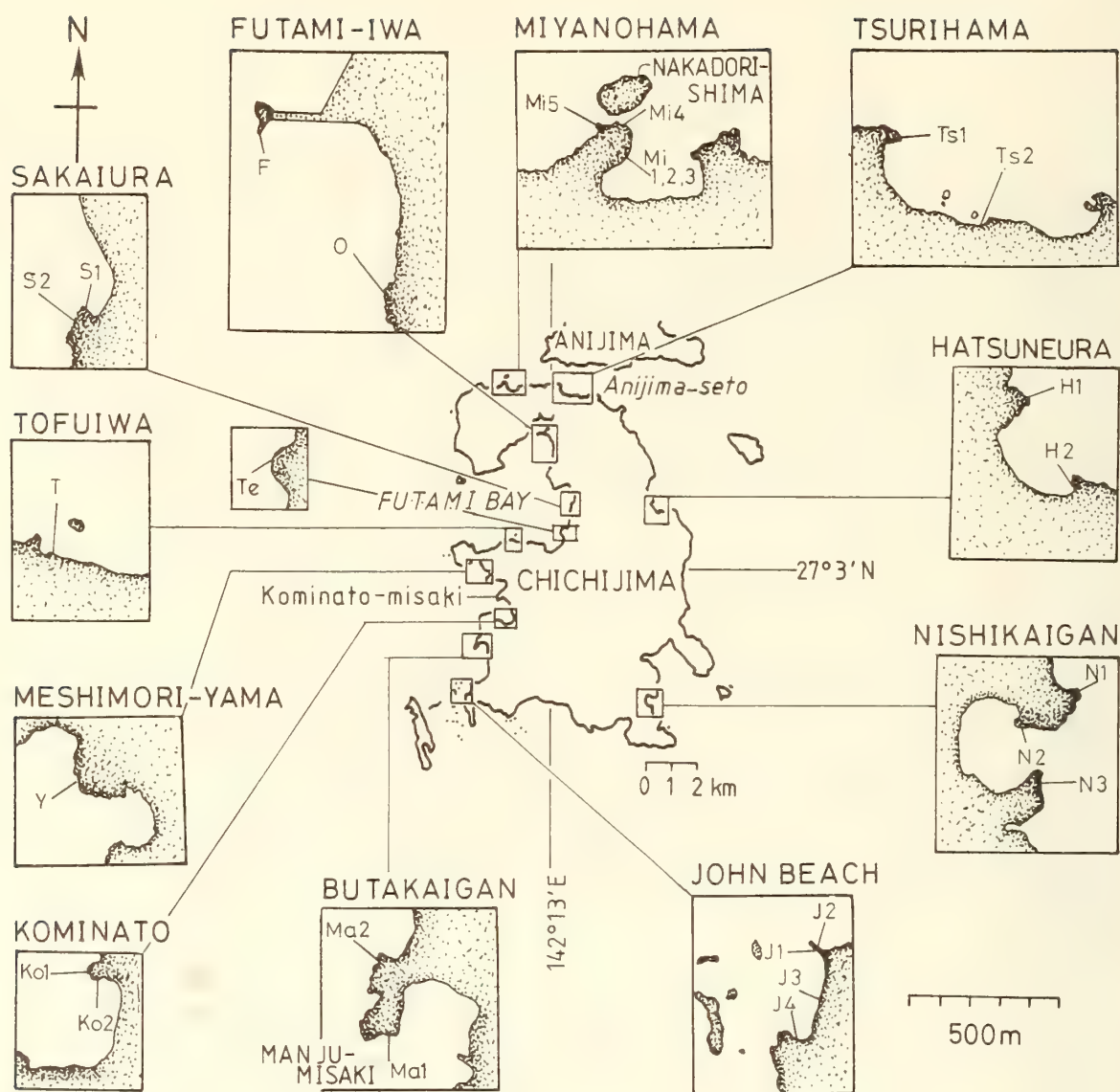


Fig. 2. Locations of the sampling points along the coast of the Chichijima Island. Abbreviations of the site names are; K: Kiyose, F: Futamiwa, O: Okumura, S1: Sakai-ura-1, S2: Sakaiura-2, Mi1: Miyano-hama-1, Mi2: Miyano-hama-2, Mi3: Miyano-hama-3, Mi4: Mi-yano-hama-4, Mi5: Miyano-hama-5, Ts1: Tsurihama-1, Ts2: Tsurihama-2, H1: Hatsuneura-1, H2: Hatsuneura-2, N1: Nishikaigan-1, N2: Nishikagan-2, N3: Nishikaigan-3, J1: John Beach-1, J2: John Beach-2, J3: John Beach-3, J4: John Beach-4, Ma1: Manjyumisaki-1, Ma2: Manjyumisaki-2, Ko1: Kominato-1, Ko2: Kominato-2, Te: Tengu-bana, T: Toufuiwa, Y: Yagyusan

COMMENTS ON SOME SPECIES

1. *Megabalanus occator* (Darwin) (Fig. 3A)

Common to the lower intertidal zone of wave-exposed rocky shores and one of the most important organisms characterizing the zonation pattern of wave-exposed rock platforms (Asakura *et al.*, 1991). This species has also been reported from the Tokara Islands and further south, but details of the geographical distribution have not yet been fully studied (Yamaguchi, 1986).

2. *Callianidea typa* H. Milne Edwards

Two specimens of this ghost shrimp were collected under a boulder in the lower intertidal zone of the Yagyusan coast. This species has been reported from Bismark Island (type locality), Kagoshima, Yaeyama Islands, and the Tokara Islands (Miyake, 1956). Recently Oishi (1970) recorded *Callianidea planocula* Melin from Futami Bay of Chichijima Island, although the species may be a synonym of *C. typa* (K. Sakai, personal communication).

3. *Pagurus insulae* Asakura (Fig. 3B)

A dominant hermit crab species of the intertidal zones from sheltered to exposed rocky shores. This species resembles *P. geminus*, but *P. geminus* has the single large tubercle on ventral surface of the merus of each cheliped, which this species does not have. One of the authors of this paper made a description of this as a new species in Asakura (1991a).

4. *Leptodius davaoensis* Ward (Fig. 3C)

(=*Leptodius leptodon* Forest & Guinot; Takeda & Miyake, 1976). Commonly found under the boulders. Takeda (1980) examined the crab specimens described by Ward in 1939 and 1941 (preserved in Am. Mus. Nat. Hist.) and revealed that *L. davaoensis* Ward, 1941 was conspecific with *L. leptodon* Forest & Guinot, 1961.

5. *Ischnochiton computus* f. *computus* Gould (Fig. 3D)

Inhabiting under boulders in the lower intertidal zone. Morphological characters of the specimens are similar to *Ischnochiton computus* Gould from the temperate Japanese region. However, all of the shells collected from Ogasawara have green color with no obvious patterns. In contrast, the shells from the Japanese temperate region have several distinct color patterns.

6. *Notoacmea schrenckii boninensis* Asakura & Nishihama (Fig. 3E)

N. schrenckii is widely distributed in temperate Japanese waters. Specimens from Chichijima Island are small in size and have a different shell color pattern from those in the temperate region. We made a description of this limpet as a new subspecies of *N. schrenckii* in Asakura & Nishihama (1987a).

7. *Monodonta australis* Lamarck (Fig. 3F)

A very abundant snail in boulder beaches. Two types of shells were found; a tall shell with numerous granules on the surface (right in Fig. 3F) and a short shell with smooth surface (only this type has been known to date [Takenouchi, 1986; Habe & Okutani, 1975])(left in Fig. 3F). The former was found in wave-sheltered beaches such as Kiyose and Okumura, and the latter was found over a wider range, from the wave-moderate to very exposed beaches. This species has also been reported from Hong Kong (Morton & Morton, 1983) and southern Africa (Branch & Branch, 1981), however there has been no record from Okinawa (the Ryukyu Islands). Recently K. Takenouchi (personal communication) found that morphological characteristics of the specimens from Ogasawara (the short type) did not fit those in the original description as well as those specimens collected from Hong Kong. The specimens may belong to a new endemic which requires taxonomic reconsideration.

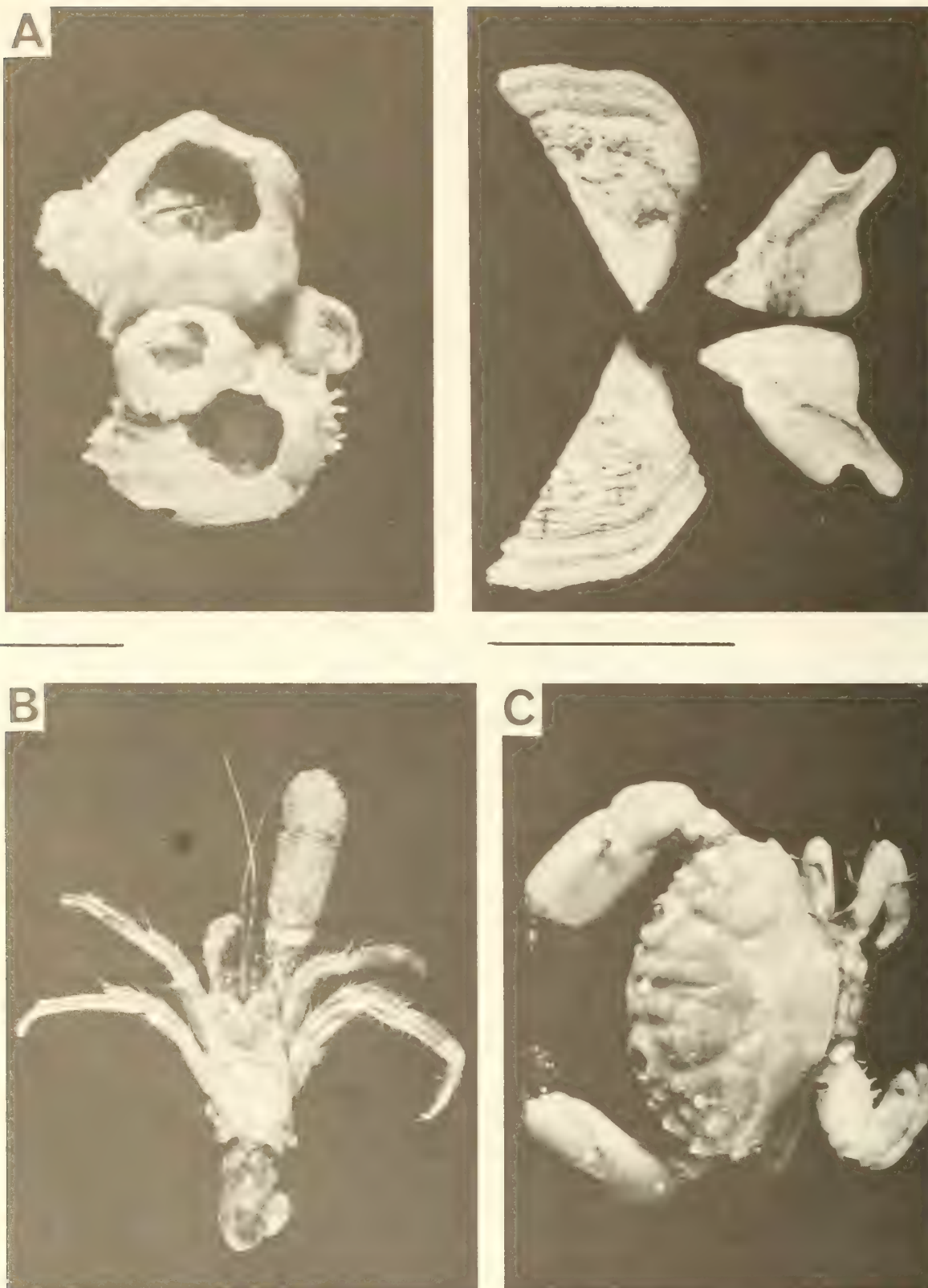


Fig. 3. Selected species characterizing the intertidal zones of the Chichijima Island. Horizontal bars indicate 1 cm. A. *Megabalanus occator* (Darwin); left: outer view, right: scutum and tergum B. *Pagurus insulae* Asakura. C. *Leptodius davaoensis* Ward.

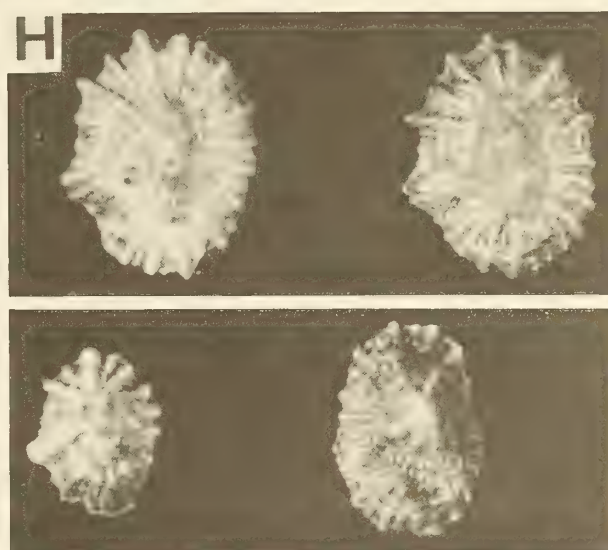
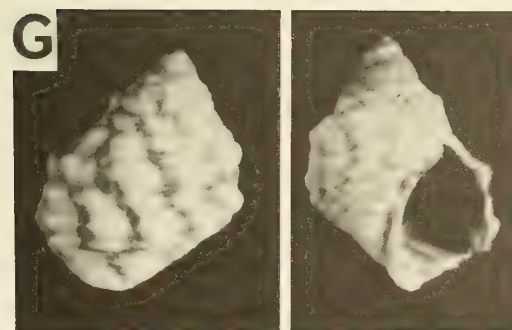
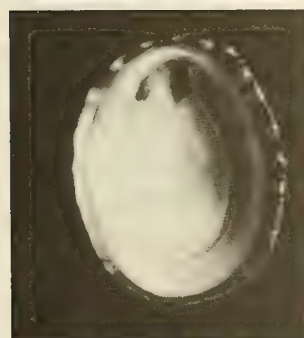
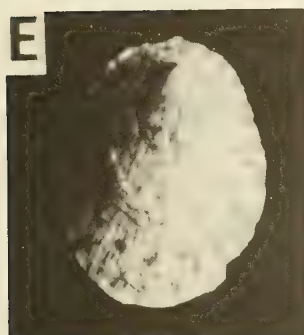
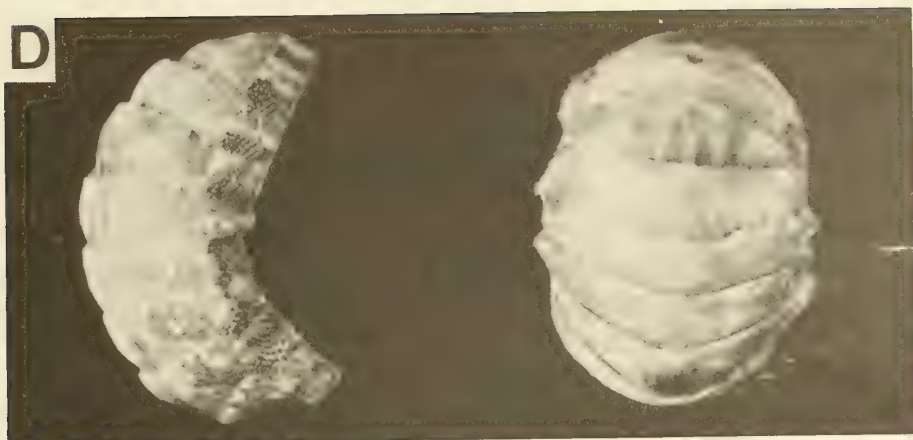


Fig. 3 (continued) D. *Ischnochiton comptus* f. *comptus* Gould. E. *Notoacmea schrenckii boninensis* Asakura & Nishihama. F. *Monodonta australis* Lamarck G. *Nodilittorina* sp. H. *Siphonaria* sp.

8. *Monodonta perplexa boninensis* Asakura & Nishihama

Abundant in boulder beaches. This subspecies is endemic to Ogasawara. Only the name was given by Pilsbry, but no valid taxonomic description was made. We described this species in comparison with *M. perplexa perplexa* in Asakura & Nishihama (1987b).

9. *Nodilittorina* sp. (Fig. 3G)

Very abundant in the upper rocky intertidal zones (Asakura *et al.*, 1991). In Japan and its adjacent waters, this species can be found only in Ogasawara, except in a very few cases in Okinawa (Habe, 1951; Nishihira, 1977). Oyama (1940) and Oyama & Takemura (1963) identified this species as *Nodilittorina miliaris*. However, Rosewater (1970) identified it as *N. leucosticta feejeensis* (Reeve), and then Rosewater & Kadolsky (1981) synonymized it as *N. quadricincta feejeensis*. Asakura & Kurozumi (1991) discussed morphological difference between the true *N. quadricincta feejeensis* and specimens from the Ogasawara. We believe that the species in the Ogasawara is endemic and taxonomic re-examination is needed.

10. *Siphonaria* sp. (Fig. 3H)

Inhabiting abundantly the rock platform surfaces and underside of boulders (Asakura *et al.*, 1990, 1991). The shell morphology of this limpet is variable. Kurata *et al.* (1969) and Shigei (1970) also recorded this species from Ogasawara. Morphologically, its shell is different from any other *Siphonaria* species in Japan and its adjacent waters, and further taxonomic study is needed (Asakura *et al.*, 1991).

LIST OF SPECIES

Abbreviations of the name of the sampling sites are as follows (see Fig. 2 for the location of each site). K: Kiyose, F: Futamiwa, O: Okumura, S1: Sakaiura-1, S2: Sakaiura-2, Mi1: Miyanohama-1, Mi2: Miyanohama-2, Mi3: Miyanohama-3, Mi4: Miyanohama-4, Mi5: Miyanohama-5, Ts1: Tsurihama-1, Ts2: Tsurihama-2, H1: Hatsuneura-1, H2: Hatsuneura-2, N1: Nishikaigan-1, N2: Nishikagan-2, N3: Nishikaigan-3, J1: John Beach-1, J2: John Beach-2, J3: John Beach-3, J4: John Beach-4, Ma1: Manjyumisaki-1, Ma2: Manjyumisaki-2, Ko1: Kominato-1, Ko2: Kominato-2, Te: Tengubana, T: Toufuiwa, Y: Yagyusan

Small capitals after the abbreviations of the site names indicate the shore types; r: steep rock platform, p: rocky shore with many tide pools, b: boulder beach, be: beachrock.

Asterisks indicate cases where only vacant shells were collected, and, for reference, species recorded solely from vacant shells are listed in Appendix 1. Specimens are deposited in the National Science Museum, Tokyo [NSMT], Amakusa Marine Biological Laboratory of Kyushu University [AMBL], and Shikoku Women's University [SWU]. Other specimens, which are not particularly indicated, are deposited in the Natural History Museum and Institute, Chiba [CBM].

Phylum Arthropoda

Class Crustacea

Subclass Cirripedia

Order Thoracica

Suborder Balanomorpha

Family Chthamalidae

Chthamalus challenger Hoek

F-r, O-r, S1-r, S2-r, Te-r, T-r, Y-r, Mi1-r, Mi2-r, Mi3-r, Mi4-r, Mi5-r, Ts1-r, Ts2-r, H1-r, H2-r, J1-r, J2-r, J3-be, N1-r, N2-r, N3-r, Ko1-r, Ko2-r, Ma1-r, Ma2-r

Family Tetracelitidae

Tetracelita squamosa japonica Pilsbry

Y-r, Ts1-r

Family Balanidae

Megabalanus occator (Darwin)

S2-r, Te-r, T-r, Y-r, Ts1-r, H1-r, N1-r, N2-r, Ma2-r

Subclass Malacostraca

Order Isopoda

Suborder Flabellifera

Family Cirolanidae

Cirolana harfordi japonica Thielemann

S2-r

Order Decapoda

Suborder Natantia

Family Alpheidae

Alpheus pacificus Dana

O-b, S1-b, Y-b

Suborder Reptantia

Infraorder Anomura

Family Porcellanidae

Petrolisthes japonicus (De Haan)

K-b, O-b, S1-b, Y-b, Ma-b

Family Callianassidae

Callianidea typa H. Milne Edwards [SWU]

Y-b

Family Diogenidae

Calcinus laevimanus (Randall)

S1-p, S2-p, S1-b, T-p, Y-p, Y-b, Ha1-p, Ha2-p, Ts1-p, Ts2-p, J1-p, J2-p, J3-be, Ma1-p, Mi3-p, Mi4-p, Mi5-p, N1-p, N2-p, N3-p, H1-p, H2-p

Calcinus gaimardii (H. Milne Edwards)

O-p

Calcinus latens (Randall)

O-p, S1-p, T-p, Y-p, N2-p, N3-p

Calcinus elegans (H. Milne Edwards)

O-p, T-p, Y-p, J1-p, J2-p, Ma1-p, H2-p, Ts1-p, Ts2-p

Calcinus guamensis Wooster

Ts2-r

Calcinus sp. 1

O-p, T-p, Y-p, Ma1-p, H1-p, H2-p, Ts1-p, Ts2-p

Calcinus sp. 2 (? *C. nitidus* Heller)

Ts2-r

Clibanarius humilis Dana

K-b, O-b, O-p, S1-p, S1-b, T-p, Y-b, Y-p, H2-p, J1-p, J2-p, Ma1-p, Ma1-b, Mi1-b, M4-p, Mi5-p, N2-p, N3-p, Ts1-p, Ts2-p

Family Paguridae

Pagurus insulae Asakura

K-b, O-p, O-b, S1-p, S1-b, T-p, Y-b, Y-p, Ko2-r, Ma1-p, Mi1-p, H2-p, N2-p, N2-b, N3-p, Ts1-p, Ts2-p

Infraorder Brachyura

Family Xanthidae

Leptodius davaoensis Ward

K-b, O-b, S1-b

Xanthias lamarchii (H. Milne Edwards)

O-b, S1-b

Family Menippidae

Epixanthus corrosus A. Milne Edwards

K-b

Family Grapsidae

Metopograpsus messor (Forskål)

K-b

Gaetice depressus (De Haan)

K-b, O-b, O-p, S1-b, S1-p, Y-b, Y-p

Sesarma dehaani H. Milne Edwards

mouth area of Kiyose river

Phylum Mollusca

Subphylum Amphineura

Class Polyplacophora

Order Neoloricata

Suborder Ischnochitonina

Family Ischnochitonidae

Ischnochiton comptus f. *comptus* (Gould) [AMBL]

O-b, O-p, S1-b, Y-b

Family Chitonidae

Onithochiton hirasei Pilsbry [AMBL]

O-p

Acanthopleura japonica (Lischke) [AMBL]

O-r, S1-r, S2-r, Te-r, T-r, Y-r, Mi2-r, Mi4-r, Ts1-r, H1-r, H2-r, J1-r, J2-r, J4-l, N1-r, Ko2-r, Ma1-r, Ma2-r

Suborder Acanthochitonina

Family Acanthochitonidae

Acanthochiton rubrolineatus (Lischke) [AMBL]

O-p

Subphylum Conchifera

Class Gastropoda

Subclass Prosobranchia

Order Archaeogastropoda

Family Patellidae

Patella flexuosa Quoy & Gaimard

Ma1-r, Ma2-r

Cellana enneagona (Reeve)

O-p, O-r, O-b, S1-r, S2-r, S1-p, S1-b, T-r, T-p, Y-r, Y-p, Y-b, Ts2-r, H2-r, J3-be, Ma2-r

Cellana mazatlandica (Sowerby) [AMBL, CBM]

O-r, S1-r, Te-r, T-r, Y-r, J1-r, J2-r, Ko2-r

Family Acmaeidae

Notoacmea schrenckii boninensis Asakura & Nishihama [NSMT, CBM]

O-b, S1-b, Y-b, Mi1-b, Ts1-b, H2-b, N2-b, Ma1-b, Ko2-b

Notoacmea cf. *concinna* (Lischke)

Y-b

Family Trochidae

Diloma suavis (Philippi)

O-r, S1-p, S1-r, S2-r, T-p, T-r, Y-p, Y-r, Ma2-r

Monodonta australis Lamarck

K-b, F-r, O-b, O-r, O-p, S1-b, S1-p, S1-r, Te-r, T-p, T-r, Y-b, Y-p, Y-r

Monodonta perplexa boninensis Asakura & Nishihama [NSMT, CBM]

Y-b, Y-p*, T-p*, O-p*

Clanculus denticulatus (Gray) ?

O-b, O-p*, T-p*, Y-p

Talopena vernicosa (Gould)

S1-b, S1-p*

Family Turbinidae

Lunella cinerea (Born)

O-b, S1-b, S1-p*, O-p*

Family Neritidae

Nerita (Ritena) plicata Linnaeus

O-r, Te-r, K-b*

Nerita (Theliostyla) squamulata (Récluz)

O-b, S1-b

Nerita (Theliostyla) albicilla Linnaeus

O-b, O-p, S1-b, S1-p, T-p, Y-b, Y-p, H2-b, N2-b, Ma1-b, Ko2-b

Nerita (Amphinerita) polita Linnaeus

Y-b

Order Mesogastropoda

Family Littorinidae

Nodilittorina pyramidalis (Quoy & Gaimard)

F-r, O-p, O-r, S1-r, S1-p, S2-r, Te-r, T-p, T-r, Y-p, Y-r, Y-b*, Mi1-r, Mi2-r, Mi3-r, Mi4-r, Mi5-r, Ts1-r, Ts2-r, H1-r, H2-r, J1-r, J2-r, J4-l, N1-r, N2-r, N3-r, Ko1-r, Ko2-r, Ma1-r, Ma2-r

Nodilittorina sp.

F-r, O-p, O-r, S1-r, S1-p, Te-r, T-p, T-r, Y-p, Y-r, Y-b*, Mi1-r, Mi2-r, Mi4-r, Mi5-r, Ts1-r, Ts2-r, H1-r, H2-r, J1-r, J2-r, J3-be, N1-r, N2-r, N3-r, Ko1-r, Ma1-r, Ma2-r

Littoraria pintado (Wood)

O-p, O-r, S1-r, S1-p, S1-b*, S2-r, Te-r, T-p, T-r, Y-p, Y-r, Mi1-r, Mi2-r, Mi4-r, Ts2-r, J4-l, N1-r, N3-r,

Littoraria coccinea (Gmelin)

S1-r, S1-b, S2-r

Family Vermetidae

Dendropoma sp.

Ts1-r, Ts2-r, H1-r, H2-r, N1-r, N2-r, N3-r, Ma1-r

Serpulorbis imbricatus (Dunker)

O-r, O-p, S1-r, S1-p, S1-b*, T-p, Y-p, Mi3-r, H1-r, H2-r, N1-r, N2-r, N3-r, Ko1-r, Ko2-r, Ma2-r

Serpulorbis daidai Schuwimmer & Nishiwaki

Mi4-r, J2-r, Ko2-r

Vermetus sp.

Mi2-r, Mi5-r, J1-r, J2-r, J3-be, Ma1-r

Family Planaxidae

Angiola inepta (Gould)

O-b, O-p, S1-b, S1-p, T-p, Y-b, Y-p

Supplanaxis niger (Quoy & Gaimard)

S1-b, Y-p, T-p

Family Naticidae

Natica lurida (Philippi)

S1-b, S1-p*, T-p*, Y-b*, Y-p*,

Order Neogastropoda

Family Muricidae

Nassa sarta (Bruguière)

Y-p, T-p*, O-p*

Mancinella siro (Kuroda)

O-p*, H1-r

Mancinella intermedia (Kiener)

Y-p, O-p*, Mi3-r, N1-r

Drupa ricinus ricinus (Linnaeus)

O-b, O-p, S1-b, S1-p, T-p, Y-p, Y-b

Drupa ricinus hadari Emerson & Cernohorsky

Y-p, T-p*

Cronia (Muricodrupa) fiscella (Gmelin)

Y-p

Maculotriton serriialis (Deshayes)

Y-p, T-p*

Morula striata (Pease)

O-p, S1-p, T-p, Y-p

Morula granulata (Duclos)

O-b, O-p, T-p, Y-p, H1-r, H2-r, N2-r, N3-r, Ma2-r

Morula borealis (Pilsbry)

T-p, Y-p

Thais (Stramonita) aculeata (Deshayes)

Y-p

Purpura panama (Röding)

Hi-r

Family Pyrenidae

Zafra pumila (Dunker)

S1-b, S1-p, O-b

Family Buccinidae

Polia undosa (Linnaeus)

O-p*, S1-b, S1-p, T-p, Y-b, Y-p

Family Mitridae

Strigatella fastigium (Reeve)

O-p*, Y-p

Subclass Opisthobranchia

Order Cephalaspidea

Family Haminoeidae

Smaragdinella calyculata (Broderip & Sowerby)

H1-r, J1-r, J4-r

Subclass Pulmonata

Order Basommatophora

Suborder Archaeopulmonata

Family Siphonariidae

Siphonaria sp.

O-b, O-p, O-r, S1-b, S1-p, S1-r, T-r, T-p, Y-r, Y-p, Mi1-r, Mi2-r, Mi3-r, Mi5-r, Ts1-r
Ts2-r, H1-r, H2-r, J1-r, J2-r, J3-be, N1-r, N2-r, N3-r, Ko1-r, Ko2-r, Ma1-r, Ma2-r

Class Bivalvia

Subclass Pteriomorphia

Order Mytiloida

Family Mytilidae

Hormomya mutabilis (Gould) [AMBL, CBM]

O-r, S1-r, S2-r, T-r, Mi4-r, Mi5-r, H1-r, Ko1-r, Ko2-r

Family Pteriidae

Pinctada sp. [AMBL, CBM]

H1-r

Family Isognomonidae

Isognomon nucleus Lamarck

F-r, O-r, S1-r, S2-r, T-r, Mi1-r, Mi2-r, Mi3-r, Mi5-r, J1-r, Ko2-r, Ma2-r

Family Ostreidae

Saccostrea mordax (Gould)

F-r, O-r, S-r, T-r, Y-r, Mi4-r, Mi5-r, Ts1-r, H1-r, J2-r, N1-r, Ko1-r, Ko2-r

Subclass Eulamellibranchia

Order Heterodonta

Family Lasaeidae

Lasaea cf undulata (Gould)

S-r

Family Tridacnidae

Tridacna maxima (Roding)

O-r, O-p, S-r, S-p, T-p, T-r

Phylum Annelida

Class Polychaeta

Family Serpulidae

Pomatoleios kraussii (Baird)

F-r, O-r, O-b, O-p, S-r, S-b, S-p, T-r, T-p, Y-r, Y-p

Family Sabellariidae

Idanthyrsus pennatus (Peters)

J4-l, Ma1-r

Phylum Echinodermata

Subphylum Asterozoa

Class Ophiuroidea

Order Gnathophiurida

Family Ophiocomidae

Ophiocoma scolopendrina Lamarck

O-p, S-p, Y-p

Subphylum Echinozoa

Class Echinoidea

Subclass Euechinoidea

Order Phymosomatoida

Family Stomechinoidae

Stomopneustes variolaris (Lamarck)

S-r, T-r, Y-r

Order Aulodonta

Family Diadematidae

Echinothrix diadema (Linnaeus)

N3-r

Order Camarodonta

Family Echinometridae

Echinometra mathaei (Blainville) [type B in Uehara *et al.*, (1990)] [AMBL, CBM]

O-b, S-b, S-r, T-r, T-p, Y-r, Y-p, M14-r, Tsl-r, N1-r, N2-r, Kol-r, Mal-r

Echinometra oblonga (Blainville)

H1-r, H2-r, J4-l, N1-r, N2-r, N3-r, Kol-r, Mal-r, Ma2-r

Heterocentrotus mammillatus (Linnaeus) [AMBL, CBM]

S-p, T-p, Y-p

Colobocentrotus mertensi (Brandt)

Y-r

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Appendix 1 The list of gastropods (Mollusca) species recorded solely from vacant shells. They were mainly used by the intertidal hermit crabs as their host shells. All of them are deposited in the Natural History Museum and Institute, Chiba (CBM).

Subclass Prosobranchia Order Archaeogastropoda: Family Liotiidae; *Liotina peroni* (Kiener), S-b, O-p; *L. semiclastratula* (Schrenck), S-b, Y-p. **Family Trochidae; *Calliostoma simodense*** Ikebe, T-p; *Ethalia guamensis* (Quoy & Gaimard), O-b; *Clanculus margaritarius* (Philippi) Y-p; *Clanculus* sp., S-b; *Trochus maculatus* Linnaeus, S-p, O-p; *Tectus* sp., S-p, O-p. **Family Turbinidae; *Homalopoma nocturnum*** (Gould), S-p; *Collonista glareosa* (Gould), O-p; **Order Mesogastropoda: Family Rissoinidae; *Alvania ogasawarana*** Pilsb-ry, Y-p. **Family Turritellidae; g. sp., S-b. Family Cerithiidae; *Clypeomorus chemnitziana*** (Pilsbry), S-b, Y-p, O-p; *C. trailli* (Sowerby), S-b, O-p; *C. humilis* (Dunker), K-b, O-b; *Clypeomorus* sp.1, K-b, O-b, O-p, S-b, S-p, Y-p; *Clypeomorus* sp.2, O-b, O-p, S-b, Y-p; *Conocerithium bavayi* (Vignal), S-b; *Ischnocerithium* sp., K-b. **Family Strombidae; *Canarium mutabilis*** (Swainson), T-p, S-p; *C. microurceum* Kira, T-p. **Family Cypraeidae; *Monetaria moneta*** (Linnaeus), Y-p; *M. annulus* (Linnaeus), Y-p; *Erosaria helvola* (Linnaeus), S-p; *Ravitriona caputserpentis* (Linnaeus), Y-p. **Family Cymatiidae; *Septa* sp., Y-p, O-p; *Lampusia aquatilis*** (Reeve), Y-p; *Turritriton kiiensis* (Sowerby), O-p. **Family Bursidae; *Bursa corrugata*** (Perry), Y-p; *B. bufonia* (Linnaeus), Y-p, O-p. **Order Neogastropoda : Family Muricidae; *Pascula benedicta*** (Melvill & Standen), T-p; *Drupella cornus* (Röding), O-p; *Cronia (Muricodrupa) fusca* (Küster), K-b; *C. (Usilla) fusconigra* (Pease), Y-p, T-p; *Morula uva* (Röding), Y-p; *Thais (Reishia) pseudodiadema* (Yokoyama), T-p; *Ergalatax contractus* (Reeve), K-b. **Family Coralliophilidae; *Coralliophila squamosissima*** (Smith), T-p, Y-p; *Coralliophila* sp., O-p. **Family Pyrenidae; *Pyrene testudinaria*** (Link), S-b, S-p, T-p, Y-b, Y-p; *P. flava* (Bruguère), Y-p; *Euplica versicolor* (Sowerby), K-b, O-b, O-p, S-b, S-p, T-p; *Anachis misera nigromaculata* (Tomlin), Y-p; *Zafrona lifuana* (Hervier), T-p. **Family Buccinidae; *Enzinopsis menkeana*** (Dunker), O-p, S-p. **Family Nassariidae; *Telasco velatus*** Gould, O-p, T-p; *Zeuxis hepaticus* (Pylteney), T-p; *Zeuxis* sp.1, S-b; *Zeuxis* sp.2, Y-p; *Alectrion glans suturalis* (Lamarch), K-b, O-b, O-p, S-b, S-p, Y-p. **Family Fascioliidae; *Latirus kandai*** Kuroda, K-b, S-b, Y-p; *Latirulus nagasakiensis* (Smith) ?, K-b, Y-p; *Benimakia fastiginda* (Reeve), S-b. **Family Mitridae; *Strigatella scutulata*** (Gmelin), T-p; *S. litterata* (Lamarck), O-p; *Vexillum unifasciatum* (Wood), O-p. **Family Turridae; *Lienardia planilabrum*** (Reeve) ?, Y-p; *Lienardia* sp.1, O-p; *Lienardia* sp.2, S-p. **Family Conidae; *Virgiconus flavidus*** (Lamarck), O-p; *Virroconus fulgetrum* (Sowerby), T-p; *V. sponsalis* (Hwass), Y-p; **Family Terebridae, g. sp., O-b, Order Heterogastropoda: Family Epitoniidae; *Gyroscala perplexa*** (Pease), Y-b; *Spiniscala japonica* (Dunker), S-b. **Family Architectonicidae; *Heliacus variegatus*** (Gmelin), K-b, O-b. **Subclass Opisthobranchia: Order Pyramidellomorpha: Family Pyramidellidae; *Odostomia* sp., Y-b; *Tiberia* sp., O-p. Order Cephalaspidea: Family Acteonidae; *Punctacteon fabreanus* (Grosse), S-p, T-p.**

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**PLANT COLONIZATION OF A RUBBLE BANK ON HERON ISLAND,
GREAT BARRIER REEF, AUSTRALIA**

BY

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ABSTRACT

Plant colonization of a rubble bank deposited on Heron Island was followed for over four years, ending when a cyclone destroyed much of the site. Two years elapsed before any plants were found, but after four years 30 species had been found, including 14 species native to Heron Island or other islands in the Capricorn group. A population of about 50,000 individuals was present by the end of the four years. Although most plants were weeds, the species which naturally dominate such sites were present and prominent. The number of species present on the site was related to logarithm of time since establishment, and the logarithm of the number of individuals present was also related to time since deposition of the rubble. Rapid colonization by native species is significant for management of coral cays.

INTRODUCTION

Coral cays are, by nature, small and often isolated patches of land subject to severe disturbance from such factors as tropical cyclones and other violent storms. Since a cay is composed entirely of material of biological origin, the vast bulk of it calcium carbonate from algal and coral skeletons, the substrate is an unusual and rather severe one (Wiens 1962). The soil has unusual chemical properties, and is especially high in calcium carbonate, which tends to limit the availability of phosphates. The physical structure of the substrate is also difficult for many plants.

The processes of plant colonization on such an apparently inhospitable place are of considerable interest. The angiosperm flora of Heron Island has been reported on a number of times

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2.

(Chaloupka & Domm 1986, Walker 1991a), permitting a study of invasion of the cay by weeds (Chaloupka & Domm 1985). The colonization of Lady Musgrave Island, another cay in the Capricorn Group south of Heron Island, has been reported by Walker 1991b. The plant species diversity of Lady Musgrave Island increased linearly from 1927 to 1989, but this was apparently an artifact of management procedures in that period, diversity varying as goat populations rose and fell.

In October 1987 a large quantity of rubble and silt excavated from the basin of the harbour at Heron Island was deposited on the south-western side of the cay, and built up until the surface was at about the level of the adjacent terrestrial vegetation, and well above spring tide levels. The upper surface was flat, with a total area of about 150m x 40m and more or less lens-shaped in outline. A rubble beach with a low bank of coarse coral fragments formed around the edge of the reclaimed area. The materials in the bank have been discussed by Gourlay (1991).

No attempt was made to vegetate or otherwise stabilize this deposit of coralline rubble. Vehicular traffic skirted the landward edge of the deposit, but an area approximately 70m long, and with an area of about 700m² was subject to little traffic: natural colonization of this area commenced about two years after the rubble was deposited. This colonization provided an opportunity to study the successional process on what amounted to an extension of a coral cay. Such an opportunity is not common, and offers the chance to explore the processes of vegetation development on a cay, processes of scientific and applied interest as exploitation of cays by tourists increases.

In March 1992 a cyclone eroded a large portion of the bank, and inundation with salt-water killed almost all the plants, bringing the study to an end.

METHODS

Heron Island was visited at intervals from December 1987 until March 1992, during which time vegetation records were made. In December 1987, December 1988, September and December 1989, March, June September and December 1990, and March and July 1991 it was practicable to count all individuals of all species on the vegetated portion of the rubble bank. In September and December 1991 it was necessary to estimate numbers of the more common species by placing two lines of quadrats at five metre intervals systematically across the area. The numbers of less common and more prominent species were, however, counted.

RESULTS

The first plants appeared on the rubble bank in December 1989, more than two years after the bank was deposited, when a total of 12 small and rather badly sand-blasted individuals of *Sisymbrium orientale* L were counted. The numbers of plants large enough to identify and found within the area is shown in Table 1, reaching a maximum of about 50,000 individuals in a total of 30 species, 14 of which were either native to Heron Island, or native to other similar islands in the Capricorn group.

The plants which colonised the rubble bank accumulated a mass of sand about themselves providing locations which were apparently particularly favourable sites for germination and establishment. The grasses, in particular *Lepturus repens*, built long-lasting sand mounds up to 30 cm high on the otherwise flat rubble surface. Sea birds, especially terns, frequented the area in large numbers.

Two of the *Casuarina equisetifolia* plants which were first noticed in November 1990 had reached heights of 75cm and 133cm respectively by September 1991. *Tournefortia argentea* plants which appeared at the same time had canopies ranging from 145cm tall and 140 cm wide to 25cm tall and 50 cm tall in September 1991: the larger plants had flowered and fruited. The root systems of one *Casuarina equisetifolia* were exposed by the storm which destroyed much of the rubble bank, and showed that root nodules were common.

The total number of identifiable plants was logarithmically related to days since creation of the rubble heap (fig. 1)

$$\ln N = -6.682 + 1.47 D \times 10^{-2}. (r^2 = 0.903, p < 1\%, F=55.6, 6 \text{ df})$$

where N is the total number of plants and D is the number of days since the rubble bank was deposited.

The total number of species colonizing the rubble (N) was related to logarithm of time since deposition (D) (fig. 2)

$$N = -316 + 47.3 \ln D \quad (r^2 = 0.966, p < 1\%, F = 173, 6 \text{ df})$$

4.

Table 1

Numbers of plants recorded on various dates from a rubble bank deposited at Heron Island in October 1987. Seedlings too small to identify are listed at the foot of the table. Species numbers refers to the cumulative number of native species, introduced species and total species reported to the given date on the rubble bank. Introduced species are indicated with an asterisk. No plants were present in September 1989. Dates indicate month and year.

Date	12.89	6.90	9.90	12.90	3.91	7.91	9.91	12.91
Species								
<i>Abutilon asiaticum</i>					3	1	1	1
<i>Achyranthes aspera</i> *						1	1	1
<i>Amaranthus viridis</i> *				1	1	0	0	0
<i>Argemone ochroleuca</i> *						10	24	10
<i>Boerhavia tetrandra</i>		2	2	5	30	160	560	330
<i>Cakile edentula</i>		10	49	37	75	62	16	30
<i>Capsella bursa-pastoralis</i> *		5	0	1	3	1	0	1
<i>Casuarina equisetifolia</i>					7	6	5	4
<i>Cenchrus echinatus</i> *					4	5	2	0
<i>Conyza bonariensis</i> *		10	60	207	250	210	50,000	30,000
<i>Coronopus didymus</i> *		3	0	0	1	20	30	100
<i>Digitaria ciliaris</i> *					2	2	0	0
<i>Eleusine brevifolia</i> *						45	420	0
<i>Eleusine indica</i> *			5	11	12	100	120	220
<i>Gnaphalium luteoalbum</i>				2	1	11	16	33
<i>Ipomoea pes-caprae</i>					2	1	1	1
<i>Lepturus repens</i>			1	3	100	100	500	550
<i>Lycopersicum esculentum</i> *							1	0
<i>Poa annua</i> *			40	3	1	1	900	1
<i>Portulaca oleracea</i>			1	14	15	1	1200	690
<i>Sesuvium portulacastrum</i>				2	8	16	7	6
<i>Sisymbrium orientale</i> *	12	18	100	8	80	250	260	630
<i>Sonchus oleraceus</i> *					2	24	500	250
<i>Solanum americanum</i> *							1	0
<i>Sporobolus virginicus</i>						4	10	10
<i>Stenotaphrum micranthum</i> *						1	0	0
<i>Thuarea involuta</i>					1	11	11	60
<i>Tournefortia argentea</i>					8	13	20	14
<i>Tribulus cistoides</i>		1	0	3	15	35	30	30
<i>Wollastonia biflora</i>							1	1

Total numbers of plants

Identified plants	12	54	264	307	700	1115	51,358	48,000
Native plants	0	13	52	59	264	417	1205	1071
Seedlings (unidentified)						30,000	4,000	
Total Plants	12	54	264	307	700	31,000	55,000	48,000

Total numbers of species

Native species	0	3	4	8	10	14	14	
Introduced species	1	5	7	8	12	16	16	
Total species	1	8	11	16	22	30	30	

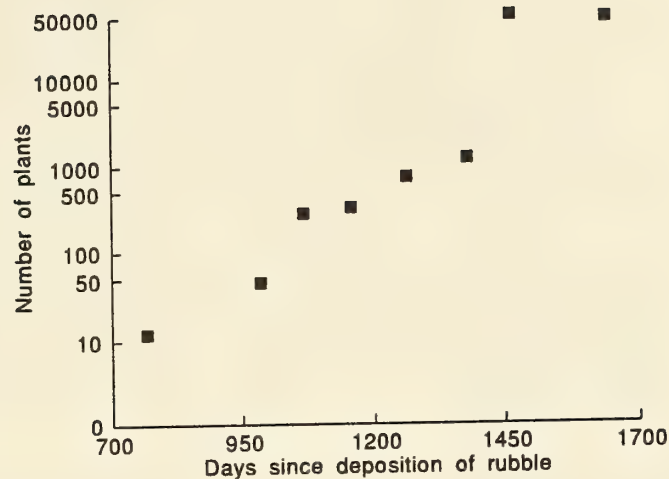


Figure 1. Number of individual plants on a rubble bank on Heron Island compared with the number of days since deposition of the rubble.

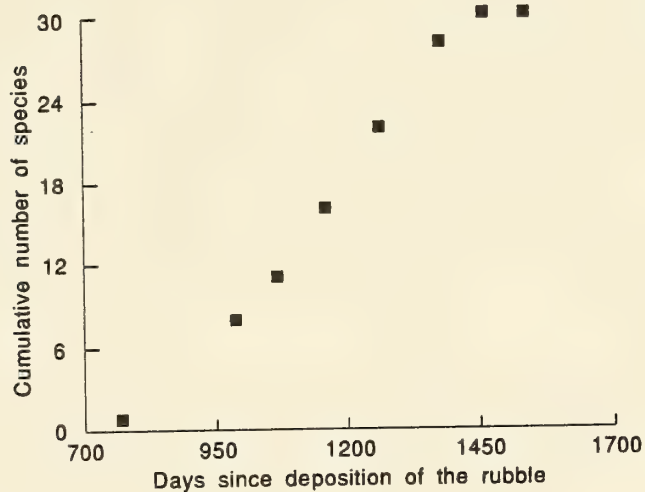


Figure 2. Cumulative number of species colonizing a rubble bank on Heron Island compared with the number of days since deposition of the rubble.

6.

The number of native species (N) fitted a similar relationship

$$N = -158 + 23.5 \ln D \quad (r^2 = 0.940, p < 1\%, F = 94.0, 6 \text{ df})$$

as did the number of introduced species (N)

$$N = -157 + 23.7 \ln D \quad (r^2 = 0.973, p < 1\%, F = 217, 6 \text{ df})$$

The more common species occurring on the site (*Boerhavia repens*, *Conyza bonariensis*, *Cakile edentula*, *Eleusine indica*, *Sisymbrium orientale*) also showed a statistically significant relationship ($r^2 > 0.70$, $p < 1\%$, $F > 55$ in each case) between time since deposition of the rubble and logarithm of total number of individuals on the site.

Of the species reported on the bank two, *Eleusine brevifolia* and *Sesuvium portulacastrum*, have not been reported previously from the island.

Discussion

The colonisation of the rubble bank was initially slow, but the number of individuals increased rapidly and logarithmically throughout the period. The number of individuals of the more common species also showed a logarithmic increase with time, none reaching a clear plateau stage or even showing a well defined drop in growth rate resulting in a logistic curve which might be expected if resources became limiting and competition for resources increased (Harper 1977). It is apparent that while the presence of some of the earlier colonizers may have facilitated the establishment of other species, succession had not proceeded to the extent that the later arrivals had begun to exclude the initial species. The appearance of long lived woody species and of perennial grasses, however, suggests that given more time displacement of populations of weedy species would proceed.

The number of species increased rapidly once colonization commenced, but slowed so that it decreased with the logarithm of time. This is entirely consistent with a logistic relationship between species richness and time available for colonization. Several species which are common on the margin of the strand had not appeared by termination of the study. *Scaevola taccada* is common on exposed shores, as is *Pandanus heronensis*, neither of which were discovered. *Scaevola taccada*, like *Tournefortia argentea* has a fleshy fruit and both are apparently bird dispersed: why only *T. argentea* has succeeded in colonising the rubble is unclear. There is no apparent biological agent to move about the large, aromatic, fleshy fruits of *Pandanus tectorius* which appear simply to fall at the base of the plant: those which fall onto a beach may then be dispersed in the sea, and fruits of *Pandanus* often found in the beach drift on Heron Island.

While the vast bulk of plants present are weeds (table 1), the native flora was well represented. Of the 30 native plants presently on the island, 13 were present on the rubble four years after deposition. *Sesuvium portulacastrum*, while not previously recorded from Heron Island is known from other Islands in the Capricorn Group, and, given the high rate of introductions and extinctions from such Islands (Chaloupka & Domm 1985) is treated as native to the Island. *Ipomoea pes-caprae* was reported on the rubble bank after a long absence from the Island (Chaloupka and Domm 1985). However, although both *Sesuvium portulacastrum* and *Ipomoea pes-caprae* appeared in an to be natural introductions to the rubble area, their recent absence perhaps being the result of a lack of appropriate natural habitats on Heron Island in recent years, both were subsequently observed growing as ground-cover plants in the gardens of the Heron Island Resort.

The three native grasses which characterize Heron Island (*Sporobolus virginicus*, *Lepturus repens*, and *Thuarea involuta*) were present and formed an extensive cover, accumulating substantial sand mounds. The long-lived perennials *Tournefortia argentea* and *Casuarina equisetifolia* which are prominent in the vegetation immediately behind the beaches of Heron Island were well established. The elements of a structured natural vegetation were, therefore, in place after about three years after the deposition of the rubble bank, and quite visually prominent after four years.

Weed populations in the disturbed area were high, and almost all of the weedy species reported from the island were found growing on the rubble bank. The appearance of numbers of *Argemone ochroleuca* on the bank was surprising, as although reported for the island by Chaloupka and Domm (1986) it has not been observed in recent years. Although no specimen was permitted to grow to maturity, young plants were found in July, September and December 1991, and in March 1992. A population in excess of 50 seeds was somehow introduced to the rubble bank, and scattered across it. It is likely that as the perennial native grass cover increased and sand accumulated on the bank, that the dominance of the short-lived weedy dicots would have decreased.

The speed with which plants recolonized such an inhospitable environment, and the diversity of species developing, has implications for the management of coral cays. Rehabilitation of a damaged cay using native species is likely to be rapid and relatively easy, provided that the source of disturbance is removed. The native species which dominate shore-lines (*Casuarina equisetifolia* and *Tournefortia argentea*) establish easily in apparently inhospitable conditions, and make rapid growth. That the native vegetation shows a rapid redevelopment is consistent with a vegetation which has evolved in a severe and periodically disturbed environment, such as a coral cay.

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ATOLL RESEARCH BULLETIN

NO. 385

IMPACT OF TOURISM-RELATED FISHING ON *TRIDACNA MAXIMA*
(MOLLUSCA, BIVALVIA) STOCKS IN BORA-BORA LAGOON
(FRENCH POLYNESIA)

BY

S. PLANES, C. CHAUVET, J. BALDWIN, J. BONVALLOT,
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**IMPACT OF TOURISM-RELATED FISHING ON *TRIDACNA MAXIMA*
(MOLLUSCA, BIVALVIA) STOCKS IN BORA-BORA LAGOON
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BY

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Abstract :

A survey of small giant clams (*Tridacna maxima*), which are subject to human predation, was carried out on the resort island of Bora-Bora in French Polynesia. This paper emphasize the impact of tourism and local activities on the *Tridacna* populations. Daily tours to the lagoon include the tasting of small giant clams. A study of clam abundance shows that the overall reef stock is still large. However a comparative analysis of the population structure of this clam, in four locations, shows a significant decrease in the average shell size of the living populations and a reduction in the average size of shells consumed by tourists. The average size of clams consumed by tourists fell from 130 mm to 108 mm in less than one year. On the fringing reef, the environmental conditions have reduced recruitment and increased natural mortality. This natural loss of giant clams along with the increasing human predation is decimating the standing stock of this area.

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Introduction

Little research has been carried out on *Tridacnidae*. The most important works are the studies by Yonge (1936) on nutrition problems and Wada (1954) on reproductive behaviours. A systematic revision by Rosewater (1965), research on the early stage of development by Labarbera (1975) and an age study by Henocque (1980), are other important contributions. Mac-Michael (1974) has studied the population structure of small giant clams at One Tree Island (Great Barrier Reef, Australia). *Tridacna maxima* (Röding, 1798) is the sole species belonging to the family *Tridacnidae* in French Polynesia. Studies on the population of the lagoon of Takapoto have been undeetailed by Ricard and Salvat (1977) and Richard (1977, 1981, 1983, 1986). More recently, studies have been completed on the ecology and aquaculture of giant clams (*Tridacna gigas*). We have considered particularly the papers of Alder and Brayley (1989), Braley (1987a, 1987b), Villanoy *et al.* (1988) and Pearson and Munro (1991), which report mortality in the natural populations of giant clams.

Bora-Bora is a small island of 30 km² in area, surrounded by a large and morphologically varied reef lagoon (Pirrazzoli *et al.*, 1985). Off the west side of the island, the lagoon is subdivided into a fairly large number of distinct depressions, which are frequently deeper than 30 m. Oceanic water enters through numerous shallow passages (hoa) all around the reef belt and returns to the open sea through the wide Teavanui pass (Fig. 1). Hotels and tourism have been well-established aspect of life on Polynesian islands like Tahiti, Moorea, Bora-Bora and some atolls for more than ten years. Tour operators now offer lagoon cruises with sea-food tasting that includes small giant clams. In 1989, a study was carried out on Bora-Bora to help the Polynesian Government to prepare a General Marine Environemental Plan (PGEM in French). During this survey, local islanders complained about the stock reduction of small giant clams.

Materials and Methods

The study was carried out from 25 March to 6 April 1990. Various transects were established in order to determine the relative abundance and the demographic structure of *Tridacna maxima* in the different reefs around Bora-Bora (Fig. 2). Along 12 barrier reef transects and 39 transects of the fringing reef, the abundance was assessed according to the following code :

0 : zero	= 0 ind./m ²
1 : low abundance	= <1 ind./m ²
2 : moderately low abundance	= 2 ind./m ²
3 : moderate abundance	= between 3 and 4 ind./m ²
4 : moderately high abundance	= 5 ind./m ²
5 : high abundance	= >5 ind./m ²

(ind. = individual)

To obtain the demographic structure, measuring of the distance between the two central bifurcating spines were made for small giant clams at each study site. An allometric relationship between this parameter and greatest shell length was calculated for the clams caught. To determine the activities affecting *Tridacna maxima*, a survey was performed with tourism professionals in Bora-Bora. Figure 3 shows a map of organized boat tours and the main sites where small giant clam tasting is offered. A special stock analysis was carried out at these sites, including sampling discarded shells on the field. Clams were studied at three main sites (Fig. 2) :

- North barrier reef (A) : this site is occasionally visited by yachtsmen, who eat clams on their boats and drop the shells at their mooring sites. Sampling was done on living molluscs and on the discarded shells.

- Fringing reef (B) : directly accessible from the shore and close to an hotel.

- South barrier reef (C and C') : "jardin de corail" is the best tourism site in Bora-Bora lagoon. Tour operators organize scuba diving and clam tasting here. We sampled both the live clams close to the shore (site C), where it is easy to walk and collect them, and also, those a little offshore in the current (site C', which this is a quite dangerous swimming place for tourists). Secondly, we measured on the discarded shells along the shore which included piles that were old (about one year) and covered by algae as well as fresh shiny shells.

The dead shells were randomly selected and measurements, similar to those made on living specimens, were taken. The number of measured shells in each site is indicated in Table 1, and an allometric relationship between the width from the two central bifurcating spines and the total length was calculated. Using statistical tests, we have compared the mean of each population in order to validate the variation between the different sites. The comparison test used the null hypothesis : $H_0 : \mu_1 = \mu_2$; and

$$Z_c = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{s_{x_1}^2}{n_1} + \frac{s_{x_2}^2}{n_2}}}$$

where \bar{x}_1 , s_{x_1} , n_1 and \bar{x}_2 , s_{x_2} , n_2 are respectively the mean, the standard deviation and the sample size of the two samples compared. The normal deviation Z_c is compared to the critical value of Z_β , where β is the error-risks ($Z(0,01)=5,14$). If $|Z_c| \leq Z_\beta$ then the means are similar and *vice et versa*.

Results

- Abundance of *Tridacna maxima*

In comparing the distribution of *Tridacna maxima* to the Bora-Bora coral area map in Galzin *et al.* (1990) we found that high densities appear on the barrier reef and in some sites in the fringing reef (Fig. 4). In the barrier reef, there is a close relationship between living coral cover and clam density. In contrast, clam density was low on most areas of the fringing reef, even with good living coral cover, and many adult and young clams were found dead in such locations.

- Demographic structure

The results of demographic structure studies are presented in Table 1, and in Figure 5. The statistical test (Z_c) used to validate the difference between the samples was found to be not significant in the analyses for the three study sites, indicating a characteristic size range for each site. In addition, Figure 5A shows a distinct low level of recruitment of young clams on the fringing reef. This might be related, in part to the harsh environmental conditions associated with the algal cover (*Acanthophora spicifera* and *Boodlea composita*) which dries out at exceptionally low tides. Another source of stress for the clam population are the activities of land reclamation and quarrying. Fifty percent of Bora-Bora's shoreline is reclaimed land and there are 12 coral quarry sites (Galzin *et al.*, 1990). Environmental disturbances associated with these activities, (lower light intensity, excessive sedimentation, low oxygen rate, etc...) contribute to the increasing the natural mortality rate of the clam population (Salvat, 1987 ; White, 1987). Moreover, fringing reefs are accessible on foot to both tourists and local inhabitants. Low density of adult stocks and low mean size of shells (75 mm) may be attributable to collecting, but low recruitment levels and natural clam mortality indicate that harsh environmental conditions must also play a part in limiting the standing stocks of giant clams.

Another interesting result is revealed in the mean size difference between living and consumed clams in sites A and C (Table 1). At both sites (A and C), the mean size of shells from consumed clams is larger indicating that human predation, which targets the largest molluscs, reduces the mean size of the live population. In the sites C and C', two other phenomena were recorded : (1) there is a reduction in the mean size of shells in the accessible living stocks (close to shore) in comparison to the inaccessible ones found offshore ($L = 79 \text{ mm}$ / $L = 89 \text{ mm}$) ; (2) there is a reduction in mean shell size of the old discarded clams, which are bigger than the recently consumed ones ($L = 130 \text{ mm}$ / $L = 108 \text{ mm}$). Thus some of the main characteristics of incipient overfishing can be documented at an individual site. These results are confirmed by the histograms in Figure 5B and 5C which show that sites C and C' have similar levels of recruitment but the shore population contains smaller individuals because they have been subjected to extensive collecting. The effect of this collecting activity is reflected in the reduction in size found between old and recently discarded shells along the shore

Discussion and Conclusion

This study was requested by the French Polynesian Ministry of the Environment and was included in overall management plan for the Bora-Bora lagoon. As a result of human activity, which is related to the site accessibility it appears that *Tridacna maxima* may have decreased in abundance in Bora-Bora.

Fringing reefs are characterised by low abundance, low recruitment and very small mean size of shells even in areas with large coral coverage that should be conducive to the development of thriving colonies of *Tridacnidae*. This low abundance could be due to both natural and human factors, the second amplifying the first. Initially, a ban on collection of clams on fringing reefs would help to preserve the adult stock. However, it will also be necessary to determine the extent and the causes for natural mortality of recruited individuals, in order to prepare a management plan conducive to the safeguard of the *Tridacnidae* in this zone.

For the most part, we have emphasized the effect of collecting activities of tourists on the clam communities. But in habitat's predation and occasional major predation by large group of people from other islands visiting for, civil or religious festivities, must be taken in account in the human predation evoked in this paper.

An analysis of flourishing barrier reef clam stocks makes it possible to measure the impact of human predation to the exclusion of other factors. The exploitation of *Tridacna maxima* causes a reduction in the mean size

of shells of living clam shells which is also reflected in the reduction in size of clams consumed by tourists. At present this predation is not significant in terms of overall abundance, but the rapid diminution in mean shell size is a point of concern.

In order to prevent the decrease of a small giant clams stock, a combination of methods (management plans, restriction on commercial trade, marine reserves, education, ...) will be required to safeguard coral reefs from the impact of human shell predation (Wells and Alcala, 1987). Studies are need to establish a size and number limit for collecting in order to ensure that giant clam stocks are not overexploited.

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	N	Lc(mm) μ et (∂)		Lt* (mm)
North barrier reef (A):				
Living population	47	24,42	(2,36)	90,68
Discarded shells	32	28,56	(2,81)	105,12
Fringing reef (B) :				
Living population	42	20,05	(2,01)	75,44
South barrier reef :				
Shore population (C) :	100	21,34	(2,12)	79,94
Offshore population (C') :	123	24,10	(2,29)	89,94
Recent shells discarded :	79	29,55	(0,90)	108,57
Old shells discarded :	80	35,83	(1,55)	130,47

Tab 1 : Population structure of *Tridacna maxima* in the three sites analysed. (N = number of shells measured ; Lc = width between the two central bifurcating spines (μ = middle-size ; ∂ = variance) ; Lt = total length estimated with the linear relation between the total length and the width between the two central bifurcating spines)

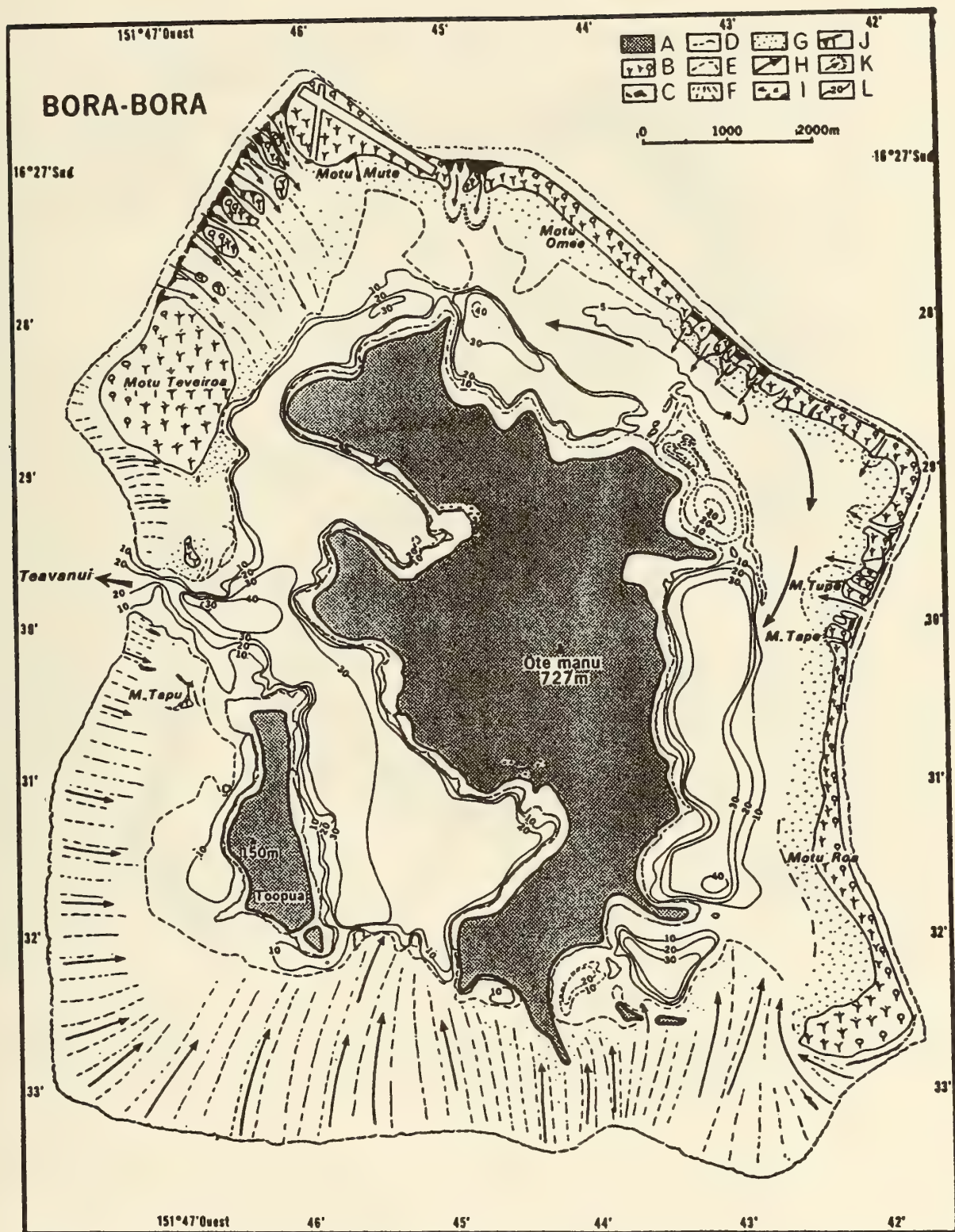


Fig 1 : Geomorphological and location map of Bora-Bora (Guilcher *et al.*, 1969). (A=volcanic islands ; B=coral island with vegetation (motu) ; C=exposed coral conglomerate ; D=outer edge of the present reef ; E=inner edge of the present reef ; F=radial lines on the reef ; G=sand ; H=direction of the main current ; I=marshes ; J=sand and gravel spits ; K=detritic delta ; L=isobathe in the lagoon (meters)).

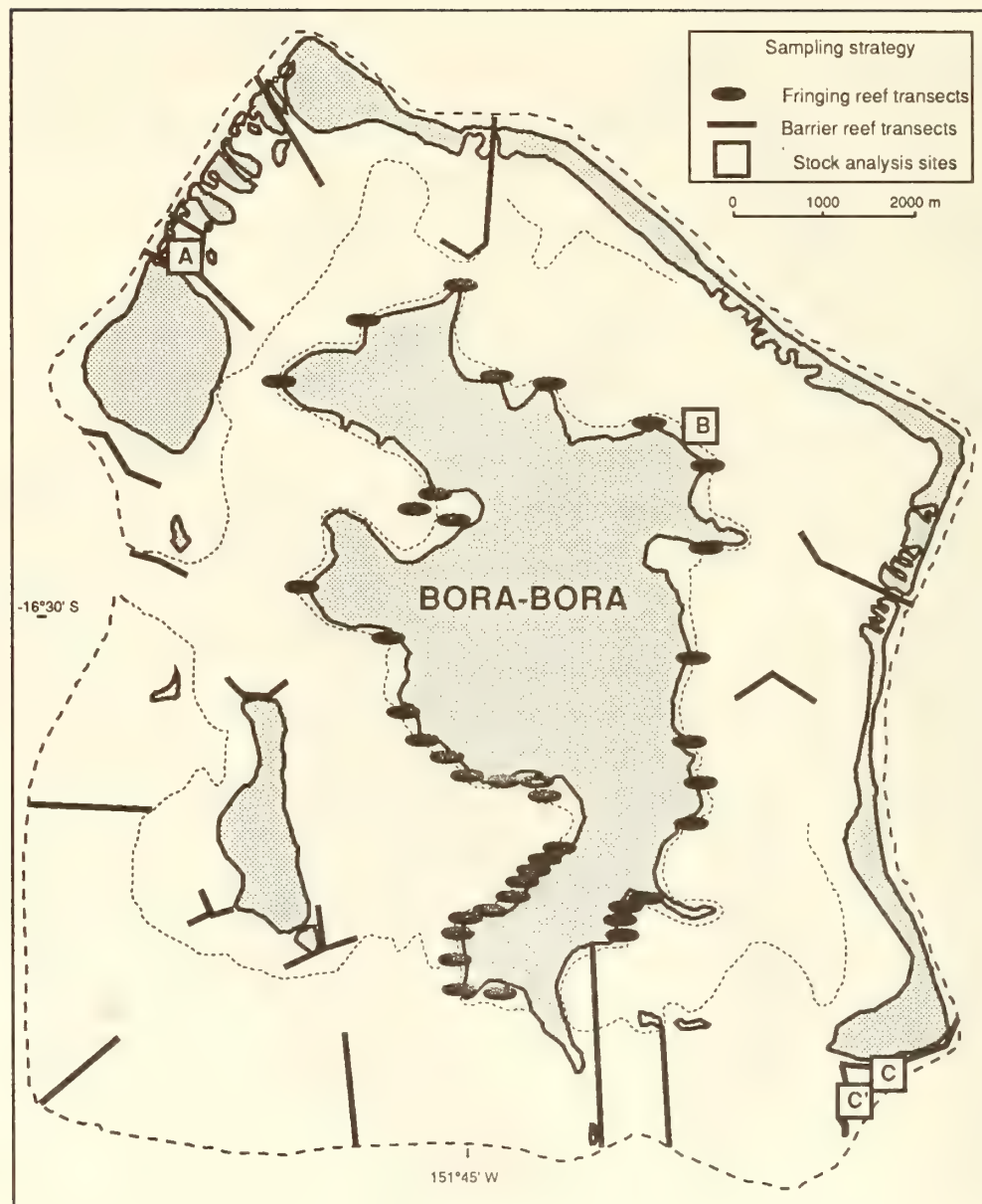


Fig 2 : Location of the 39 fringing reef transects, the 12 barrier reef transects and the four stock analysis sites.

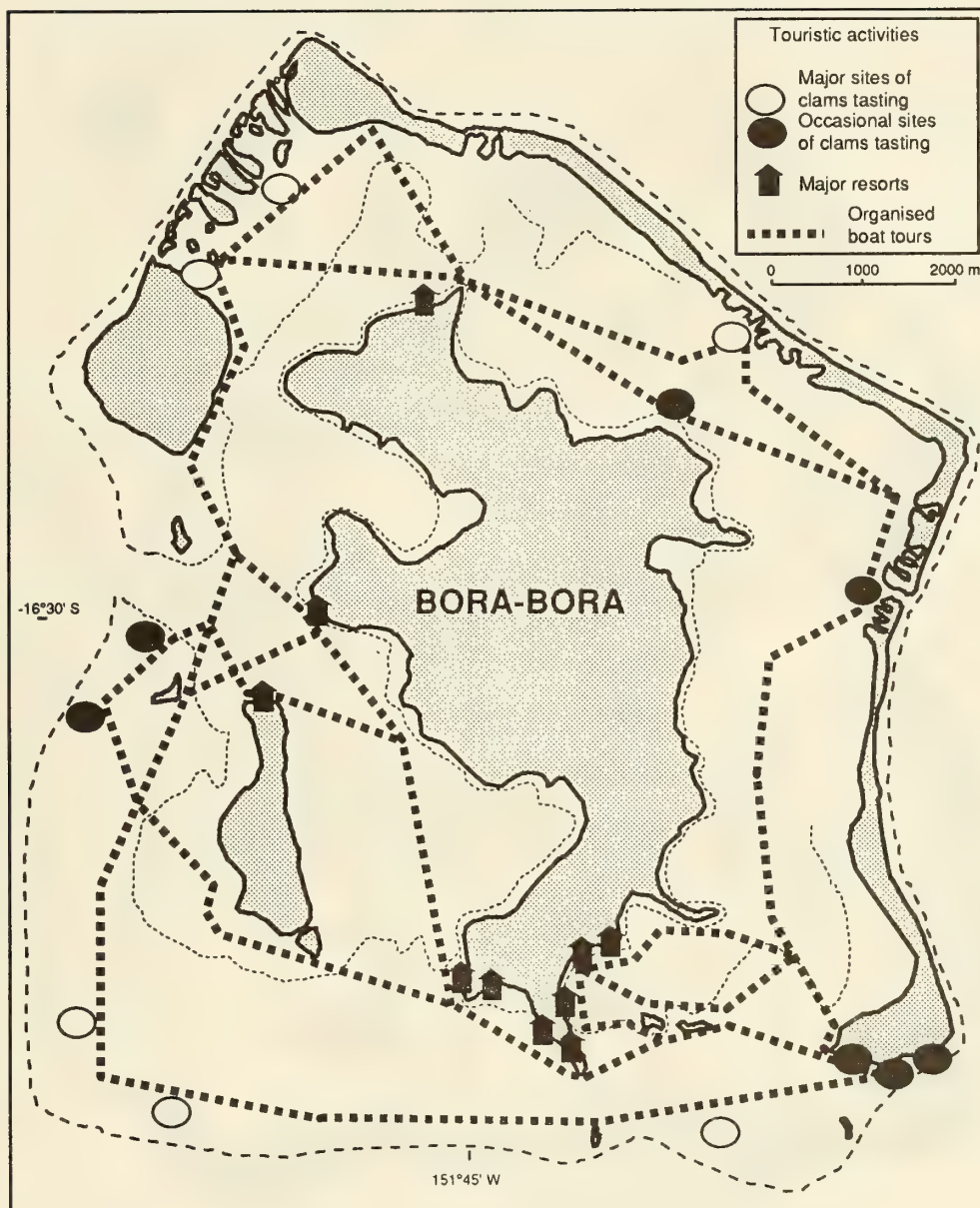


Fig 3 : Map indicating the tourist activities in the lagoon of Bora-Bora in relation to the small giant clams.

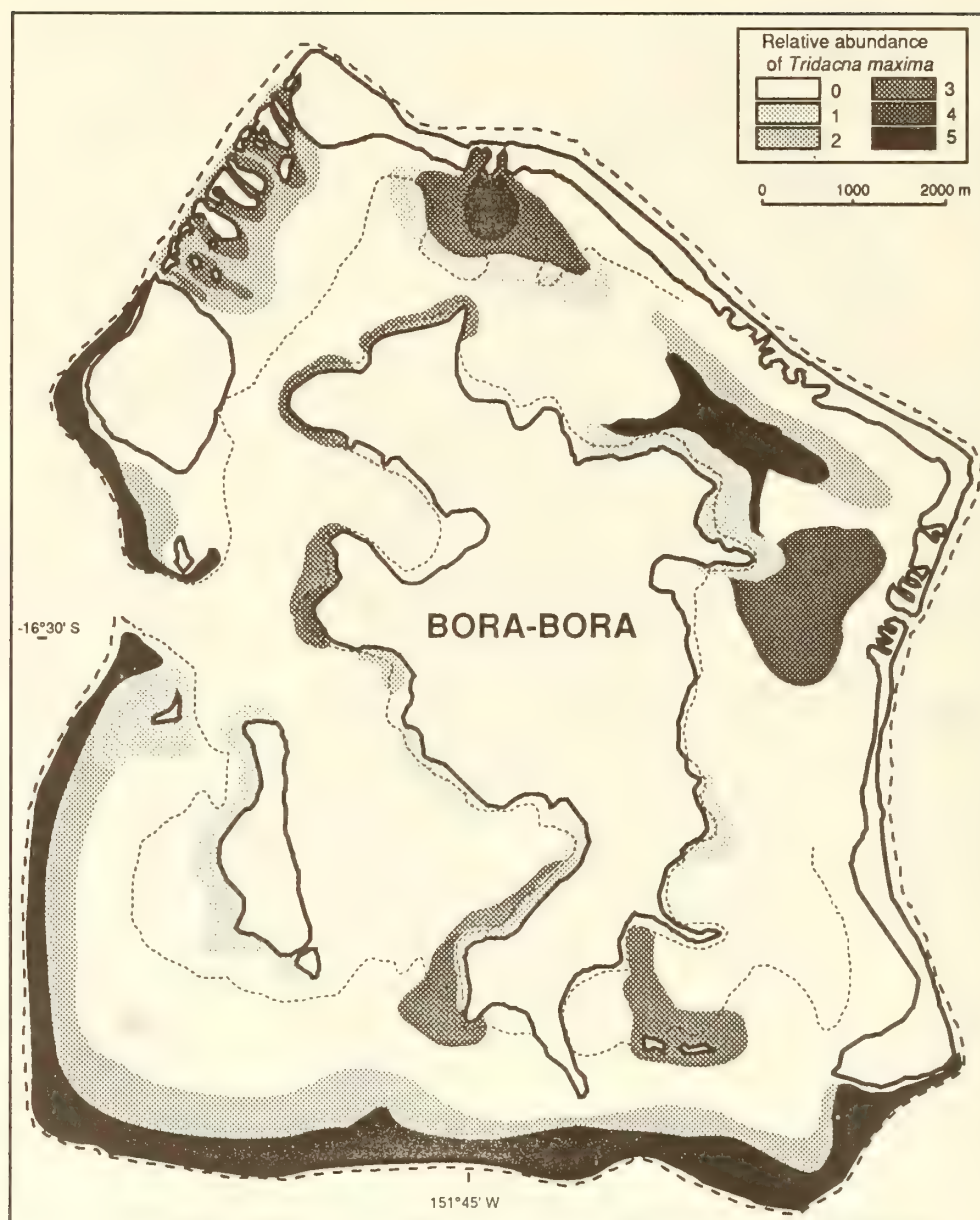


Fig 4 : Relative abundance of *Tridacna maxima* in the lagoon of Bora-Bora according to the code established.

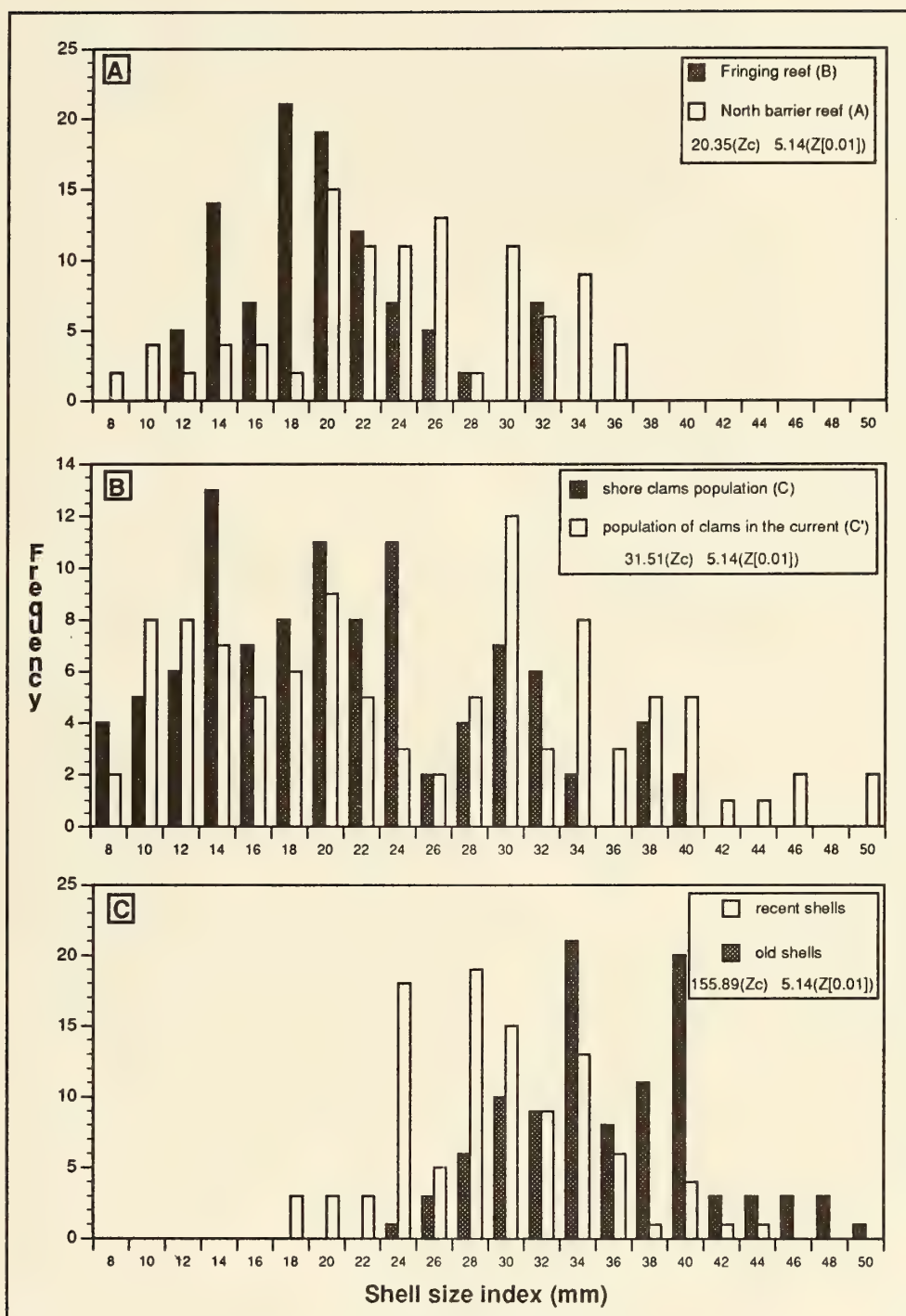


Fig 5 : Comparison of the distribution of the size frequencies of clams from different sites and statistical test on the middle-size (Z_c) :

A : Comparison between living populations in the fringing reef (B) and in the barrier reef (A).

B : Comparison between the living population near the shore (C) and the living population in the current (C').

C : Comparison between the size frequencies of shells collected one year ago and the shell recently collected.

ATOLL RESEARCH BULLETIN

NO. 386

MANGROVE SWAMPS IN BERMUDA

BY

MARTIN L.H. THOMAS

**ISSUED BY
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MANGROVE SWAMPS IN BERMUDA

BY

MARTIN L.H. THOMAS

Abstract

Bermudian mangrove swamps at 32°N are floristically similar to those in the Gulf of Mexico at 23°N, both being composed of the red mangrove, *Rhizophora mangle*, the black mangrove, *Avicennia germinans* and the buttonwood, *Conocarpus erectus* with the Brazil pepper tree, *Schinus terebinthifolia* invading. The most frequent associated flora are the red alga, *Bostrychia montagnei* and green algae *Rhizoclonium riparium* and *R. kernerii* and the flowering plants, *Asparagus sprengeri*, *Borrchia frutescens* and *Sesuvium portulacastrum*. The faunal components are very diverse and vary greatly among swamps. Mangroves of coastal bays show typical plant zonation but the tree stands of inland saltwater ponds are typically monospecific with either *R. mangle* or *A. germinans*, and the associated flora and fauna very sporadic. Once established, red or black mangroves resist invasion and occupy a zone characteristic of both species.

INTRODUCTION

The mangroves of Bermuda at 32°N are the most northern in the Atlantic (Chapman 1977), their presence being fostered by the warm waters of the Gulf Stream which give the islands a warm, frost free climate (Anon. 1974, Morris *et al.* 1977). In the North Pacific, mangroves occur as far north as 35°N in Japan and on a world-wide basis those furthest from the equator are at 37°S in New Zealand (Walsh 1974). The Bermuda mangroves are isolated, generally small in size and confined to an archipelago of very small land area. The only large swamps are the so-called "Great Mangrove" of Hungry Bay and another around Mangrove Lake (Fig. 1). Bermuda mangroves like other isolated and outlying examples, for example in Japan and New Zealand (Walsh 1974) are low in tree diversity. Only three species occur, *Rhizophora mangle* L., the red mangrove, *Avicennia germinans* (L.) L., the black mangrove and *Conocarpus erectus* L., the buttonwood (Britton 1918). Early accounts that included the white mangrove, *Laguncularia racemosa* Gaertner (Lefroy, 1884) are probably in error (*C. erectus* being locally called the "white mangrove") even though more recent accounts still include it (Verrill 1902, Hanlon *et al.* 1975). The mangrove communities of Bermuda have never been described but aspects of plant components were mentioned by Verrill (1902), Harshberger (1905), Britton (1918) and Taylor (1960). Sterrer (1986) describes many of the commoner fauna and flora.

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An unusual feature of the mangrove swamps of Bermuda is that about one third of them are located around inland salt-water ponds, the majority of which are tidal and connected to the sea by submarine fissures. These are anchialine pools according to Por (1985).

Although mangrove communities in Bermuda have not been mapped before, there is no doubt that they were formerly much more widespread. They are mentioned in early writings (eg. Lefroy 1884, Verrill 1902) and place names, still currently used, reflect their former presence. For instance, there are now no longer any mangroves in "Mangrove Bay" on the west coast. Mangrove bark was used by early settlers in tanning as well as for fuel, additionally they were cleared for coastal development (Hayward *et al.* 1981). Once cleared, mangroves are generally slow to recover (Macnae 1968).

MATERIAL AND METHODS

The locations of mangrove swamps in the Bermuda Islands was determined by reference to 1:2500, Series E811 topographic maps of Bermuda, information from the Bermuda Dept. of Agriculture and Fisheries, and by personal inspection of likely locations. Fringing mangroves, on rocky shores, dominated by *C. erectus* were not considered as swamps.

At each location where there were more than 10 trees containing either or both of *R. mangle* and *A. germinans*, the perimeter of the swamp was mapped by measurement and the use of optical rangefinders, with reference to landmarks appearing on topographic maps. The edge was defined as the outer limit of the canopy of trees or the community of halophytic plants typical of mangroves, whichever extended further. Areas were determined from the maps produced. One to 25 line transects, depending on the size of the swamp were run at right angles to the general shoreline, at low tide, from the back of the mangrove to either, the seaward extent of the canopy, the centre of the main drainage channel, or the opposite side of the swamp, depending on site characteristics. On each transect, elevation levels were determined at points where the gradient changed or at 5 m intervals, whichever was less, by optical leveling and, beyond the water line, by depth. For bay and lagoonal tidal sites (Table 1), heights were corrected to chart datum, by the method of Anon. (1985). For anchialine ponds, tide readings were taken from staff gauges installed in each pond (Thomas *et al.* 1991) and corrected to a datum of mean low tide level. For non-tidal sites, datum was taken as the normal water level. Along each transect, the first and last occurrences of all macroscopic species were measured. For mangrove trees the following additional points were fixed: the start and end of *A. germinans* pneumatophores, canopy, trunks and seedlings; the start and end of *R. mangle* prop roots, canopy, trunks and seedlings; and for *C. erectus* and *Schinus terebinthifolia* (L.) the limits of the canopy. At five meter intervals, starting at the landward edge, for each tree species, the heights of the upper and lower canopies were measured. Mangrove abundance was counted in 9-25 m² plots at 3-9 m, intervals depending on the transect length. Maximum trunk diameters at 1.5 m above ground were measured on large specimens. The general character of the

substrate was noted. Frequency data herein is the percentage of sites at which the species were found.

The scientific names of species follow Sterrer (1986) wherever possible. Specimens are deposited in the collections of the University of New Brunswick, and the experts mentioned in the acknowledgements assisted with identifications.

RESULTS

The locations of the 33 mangrove swamps surveyed (Fig. 1) are listed together with their local names and areas along with the mangrove tree species present and whether the site is a coastal bay, lagoon, anchialine pond, non-tidal pond or landlocked and non-aquatic (Table 1). The species found and their frequency of occurrence among the 33 swamps and summaries of the vertical zonation of dominant species in bay and lagoonal (marine) sites found growing above chart datum are given in Tables 2 and 3 respectively. Pond mangroves are not included in this table because the very variable, and often much reduced tidal regime among ponds makes direct correlation difficult. A composite vertical profile of all marine mangroves is shown in Fig. 2a, while Figs 2b and c show Ireland Island Lagoon [#1 Fig. 1, Table 1] and Riddels Bay [#9] as examples of the range of profiles surveyed. Profiles from three pond sites (Fig. 3) include a "mixed" mangrove at Evans Pond (3a)[#7], a red mangrove dominated situation at Mangrove Lake (3b)[#18], and the black mangrove dominated Lovers Lake (3c)[#28]. Profiles of two unique mangrove swamps are the mangrove-salt marsh complex at Mill's Creek [#12] (Fig. 4a) and the "Great Mangrove" of Hungry Bay [#16] (Fig. 4b).

Table 1. Comparison of mangrove swamps of Bermuda: mangrove tree species present, type of habitat and area occupied.

Key to terms: R = *Rhizophora mangle*; B = *Avicennia germinans*; BU = *Conocarpus erectus*; Lagoon = marine with restricted connections with the sea; Pond = saline, non-tidal pond; An. Pond = anchialine (tidal) pond; Land = landlocked without pond.

Site #	Name	Trees	Type	Area(m ²)
1	Ireland Island	R,B,BU.	Lagoon	7109
2	Head of the Scaur	R,B,BU.	Bay	189
3	Somerset Long Bay	R,B,BU.	Pond	2020
4	Elys Harbour	R,B.	Bay	5381
5	Pilchard Bay	R,B,BU.	Bay	9141
6	Whale Island	R,B,BU.	Bay	845
7	Evans Pond	R,B,BU.	An. Pond	4432
8	Jew's Bay	R,B,BU.	Bay	800
9	Riddels Bay	R,B,BU.	Bay	11568
10	Tom Wood's Bay	R,B,BU.	Bay	1781
11	Fairyland Creek	R,B,BU.	Bay	7989
12	Mill's Creek, Boss's Cove	R,B,BU.	Bay	10907

13	Paget Marsh	R.	Pond	12140
14	Foot of Crow Lane	R,B.	Bay	2336
15	Mangroville	R,B.	Pond	224
16	Hungry Bay	R,B,BU.	Bay	29717
17	Spittal Pond	B,BU.	Pond	229
18	Mangrove Lake	R,BU.	An. Pond	22597
19	Trotts Pond	R,BU.	An. Pond	8368
20	Compston Pond	R.	Pond	2900
21	Shelly Bay Mangrove	R,BU.	An. Pond	8500
22	Commonland Marsh	B,BU.	Land	800
23	Walsingham Pond	R,B,BU.	An. Pond	4933
24	Walsingham Bay	R,B,BU.	Bay	3776
25	Blue Hole	R,B,BU.	Bay	3003
26	Coney Island	R,B,BU.	Bay/Pond ¹	1755
27	Tuckers Town Bay	R,B,BU.	Bay	400
28	Lovers Lake	B,BU.	An. Pond	2288
29	Mangrove Bay	R,B,BU.	Bay	2837
30	Coot Pond	R,B,BU.	Bay	1643
31	Paget Island Pond	R,B,BU.	Bay ²	1594
32	Ferry Point	R,B,BU.	Bay	2200
33	U.S. Naval Air Base	R,B.	Pond ³	850
<hr/>				
TOTAL				175252
Mean				5310±6495

¹ Former pond with channel cut to the sea.

² Former bay, now divided by causeway.

³ Former bay, now a pond.

Table 2. Check-list of plant and animal species and the percentage of localities at which they were collected in all Bermuda mangrove swamps.

SPECIES	%	SPECIES	%
CYANOBACTERIA			
<i>Entophysalis deusta</i>	3	<i>Scytonema hofmannii</i>	6

Oscillatoria lutea 12

CHLOROPHYTA

<i>Acetabularia crenulata</i>	9	<i>Cladophora expansa</i>	12
<i>Anadyomene stellata</i>	3	<i>Halimeda incrassata</i>	6
<i>Avrainvillea nigricans</i>	3	<i>Halimeda monile</i>	6
<i>Boodleopsis pusilla</i>	3	<i>Monostroma oxyspermum</i>	15
<i>Caulerpa mexicana</i>	3	<i>Penicillus capitatus</i>	6
<i>Caulerpa peltata</i>	3	<i>Rhizoclonium hookeri</i>	3
<i>Caulerpa racemosa</i>	3	<i>Rhizoclonium kernerii</i>	48
<i>Caulerpa sertularioides</i>	6	<i>Rhizoclonium riparium</i>	55
<i>Caulerpa verticillata</i>	3	<i>Udotea flabellum</i>	6
<i>Chaetomorpha linum</i>	12	<i>Valonia macrophysa</i>	3

RHODOPHYTA

<i>Acanthophora muscoides</i>	3	<i>Ceramium rubrum</i>	3
<i>Amphiroa fragilissima</i>	3	" <i>Falkenbergia hillebrandii</i> " stage of <i>Asparagopsis</i>	3
<i>Bostrychia binderi</i>	6	<i>Halymenia bermudensis</i>	3
<i>Bostrychia montagnei</i>	94	<i>Laurencia obtusa</i>	3
<i>Bostrychia tenella</i>	3	<i>Wurdemannia miniata</i>	3

PHAEOPHYTA

Sargassum bermudense 3

MAGNOLIOPHYTA

<i>Akebia quinata</i>	3	<i>Nerium oleander</i>	6
<i>Asparagus plumosus</i>	9	<i>Opuntia dillenii</i>	3
<i>Asparagus sprengeri</i>	36	<i>Pittosporum undulatum</i>	9
<i>Avicennia germinans</i>	73	<i>Rhizophora mangle</i>	85
<i>Borrchia arborescens</i>	12	<i>Ruppia maritima</i>	3
<i>Borrchia frutescens</i>	30	<i>Sabal bermudana</i>	6
<i>Carpobrotus chilensis</i>	3	<i>Salicornia perennis</i>	21
<i>Casuarina equisetifolia</i>	6	<i>Schinus terebinthifolia</i>	42

<i>Coccoloba uvifera</i>	6	<i>Sesuvium portulacastrum</i>	33
<i>Conocarpus erectus</i>	22	<i>Syringodium filiforme</i>	15
<i>Ficus lentiginosa</i>	3	<i>Tamarix gallica</i>	12
<i>Foeniculum foeniculum</i>	3	<i>Tamarix hispida</i>	6
<i>Halodule bermudensis</i>	6	<i>Thalassia testudinum</i>	15
<i>Ipomoea</i> sp.	6	<i>Typha angustifolia</i>	3
<i>Leucaena glauca</i>	3	<i>Wedelia perfoliata</i>	33
<i>Musa cavendishii</i>	3		

PORIFERA

<i>Acervochalina molitba</i>	3	<i>Leucetta imberbis</i>	3
<i>Acervochalina crassiloba</i>	3	<i>Lissodendoryx isodictyalis</i>	3
<i>Aplysilla longispina</i>	3	<i>Megalopastas nux</i>	3
<i>Biemna microstyla</i>	3	<i>Mycale microsigmatosa</i>	3
<i>Chondrilla nucula</i>	3	<i>Niphates erecta</i>	3
<i>Cinachyrella apion</i>	5	<i>Oceanapia coela</i>	3
<i>Desmascula desdemona</i>	3	<i>Suberites</i> sp.	6
<i>Dysidea etheria</i>	3	<i>Tedania ignis</i>	3
<i>Eurypon clavatum</i>	3	<i>Terpios aurantiaca</i>	6
<i>Geodia gibberosa</i>	3	<i>Tethya actinia</i>	6
<i>Hymeniacidon</i> sp.	3	<i>Ulosa ruetzleri</i>	6
<i>Leucandra aspersa</i>	3		

CNIDARIA

<i>Aiptasia pallida</i>	9	<i>Cassiopea xamachana</i>	21
<i>Bartholomea annulata</i>	6	<i>Palythoa mammilosa</i>	3

ANNELIDA

<i>Arenicola cristata</i>	9	Sabellidae	6
Spirorbidae	9		

MOLLUSCA

<i>Assimineia succinea</i>	6	<i>Littorina angulifera</i>	15
<i>Batillaria minima</i>	15	<i>Melampus coffeus</i>	9

<i>Brachydontes domingensis</i>	3	<i>Mitrella ocellata</i>	15
<i>Cerithium lutosum</i>	15	<i>Ovatella myosotis</i>	3
<i>Hydrobia bermudae</i>	6	<i>Pedipes mirabilis</i>	3
<i>Isognomon alatus</i>	6	<i>Truncatella caribaeensis</i>	6
<i>Lasaea adansoni</i>	6		

BRYOZOA

<i>Amathia vidovici</i>	3	<i>Watersiporia subovoidea</i>	6
<i>Bugula neritina</i>	6	<i>Zoobotryon verticillatum</i>	3
<i>Schizoporella serialis</i>	6		

ARTHROPODA

<i>Alpheus</i> sp.	3	<i>Ligia baudiniana</i>	15
<i>Callianassa branneri</i>	3	<i>Mithrax forceps</i>	3
<i>Callinectes sapidus</i>	3	<i>Nephila clavipes</i>	33
<i>Cardisoma guanhumi</i>	6	<i>Pachygrapsus gracilis</i>	33
<i>Clibanarius tricolor</i>	6	<i>Panopeus herbstii</i>	3
<i>Garteracantha</i> sp.	30	<i>Sesarma ricordi</i>	6
<i>Gecarcinus lateralis</i>	9	<i>Stenopus hispidus</i>	3
<i>Goniopsis cruentata</i>	33		

ECHINODERMATA

Synaptula hydriformis

6

TUNICATA

<i>Aplidium bermudae</i>	3	<i>Ecteinascidia conklini</i>	6
<i>Aplidium exile</i>	3	<i>Ecteinascidia turbinata</i>	6
<i>Botrylloides nigrum</i>	3	<i>Leptoclinum macdonaldi</i>	3
<i>Clavelina oblonga</i>	3	<i>Perophora viridis</i>	3
<i>Clavelina picta</i>	3	<i>Phallusia nigra</i>	3
<i>Cystodytes dellechiaiei</i>	3	<i>Polycitor capsulatus</i>	3
<i>Didemnum candidum</i>	6	<i>Styela plicata</i>	3
<i>Distaplia bermudensis</i>	3		

CHORDATA

<i>Anolis grahami</i>	24	<i>Eleutherodactylus johnstoni</i>	33
<i>Bufo marinus</i>	12	<i>Malaclemys terrapin</i>	6
<i>Chelonia mydas</i>	3		

Table 3. Mean vertical zones above low-water level and their standard deviations, of the dominant plant species in Bermudian bay and lagoon mangrove swamps. Tidal heights are in cm above chart datum.

Species	Part of plant	Tidal Heights	
		Lower Limit	Upper Limit
<i>Rhizophora mangle</i>	Prop Roots	22.0 \pm 16.9	80.7 \pm 25.7
<i>Rhizophora mangle</i>	Canopy ¹	11.3 \pm 14.6	110.7 \pm 66.2
<i>Rhizophora mangle</i>	Trunks ¹	33.0 \pm 16.3	70.0 \pm 17.8
<i>Avicennia germinans</i>	Pneumat.	34.7 \pm 13.0	85.3 \pm 26.8
<i>Avicennia germinans</i>	Canopy ¹	26.0 \pm 22.5	148.3 \pm 76.7
<i>Avicennia germinans</i>	Trunks ¹	48.7 \pm 14.1	84.7 \pm 29.4
<i>Conocarpus erectus</i>	Canopy ¹	82.5 \pm 53.0	307.5 \pm 145.0
<i>Conocarpus erectus</i>	Trunks ¹	125.0 \pm 7.1	267.5 \pm 109.6
<i>Schinus terebinthifolia</i>	Canopy ¹	116.7 \pm 37.9	150.0 \pm 60.6
<i>Schinus terebinthifolia</i>	Trunks ¹	140.0 \pm 52.2	151.7 \pm 47.3
<i>Bostrychia montagnei</i>	Entire	25.0 \pm 22.3	71.0 \pm 17.1
<i>Rhizoclonium kernerii</i>	Entire	38.8 \pm 24.9	68.8 \pm 17.5
<i>Rhizoclonium riparium</i>	Entire	31.3 \pm 20.7	96.3 \pm 25.1
<i>Borrchia frutescens</i>	Entire	85.0 \pm 24.5	133.8 \pm 40.9

<i>Sesuvium portulacastrum</i>	Entire	68.0 \pm 20.8	106.0 \pm 47.2
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¹At sediment surface vertically below limit.

For comparison, tidal levels are: Mean Low Tide Level 30 cm, Mean Tide Level 70 cm, Mean High Tide Level 105 cm and Extreme High Tide Level 150 cm.

The average bay or lagoonal mangrove in Bermuda is about 25m wide, dominated intertidally by *R. mangle* and *A. germinans*, the former forming the seaward fringe and the latter the mid-portion of the community, but usually with considerable overlap. Above the high-tide mark, *C. erecta* and *S. terebinthifolia* intermingle on rising drier ground. The height of the canopy top for these four species lies between 5 and 6 m. On prop-roots and pneumatophores in the lower to mid-intertidal, the red alga *Bostrychia montagnei* Harvey is ubiquitous together with the green filamentous alga *Rhizoclonium kernerii* Stockmeyer, whereas *R. riparium* Harvey occurs in patches throughout the intertidal but not generally on the mangroves. *Sesuvium portulacastrum* L. is scattered above mean tidal level, giving way to an irregular band of *Borrchia frutescens* (L.) A. P. de Candolle around high tide mark. A wide variety of associated fauna and flora were found but none were regular and many were at a single location only (Table 2). The best developed and most diverse mangrove is at Hungry Bay on the south shore (Fig. 4a). This is the only Bermuda mangrove with a well developed drainage channel. The width of the swamp reaches 90 m, the canopy height exceeds 10 m in places, and there is no zonation among red and black mangroves, which are completely intermingled. The giant land crab, *Cardisoma guanhumi* Latreille, rare in Bermuda is common on the landward fringe, and the coffee-bean marsh snail, *Melampus coffeus* (L.), is found at only three locations, abundant in the upper intertidal. Trunk diameters of mangrove trees were largest here, with *A. germinans* reaching 36 cm and *R. mangle* to 27 cm.

The structure of pond mangroves (Fig. 3) differs considerably from that of bay mangroves. They are narrower, only 14.8 \pm 11.2 m wide compared to 30.6 \pm 20.1 for bay mangroves, but have a similar canopy height and are more varied. Mono-specific stands of either *R. mangle* or *A. germinans*, are typical (Table 2) in Bermuda ponds, but red and black mangroves are sympatric in Evans pond and Walsingham Pond. However, in Evans Pond, black mangroves dominate and red mangroves are scattered individuals except at the eastern end (see profile Fig. 3a). In the largest pond mangroves of Mangrove Lake and Trotts Pond, black mangroves are absent, as they are at the smaller Compston Pond and they are not abundant at Walsingham Pond. In contrast at Lovers Lake, red mangroves are absent. In the former pond (now connected to the sea) at Paget Island, red mangroves are confined to a few young trees at the seaward margin of the swamp, suggesting an earlier monospecific stand of *A. germinans*.

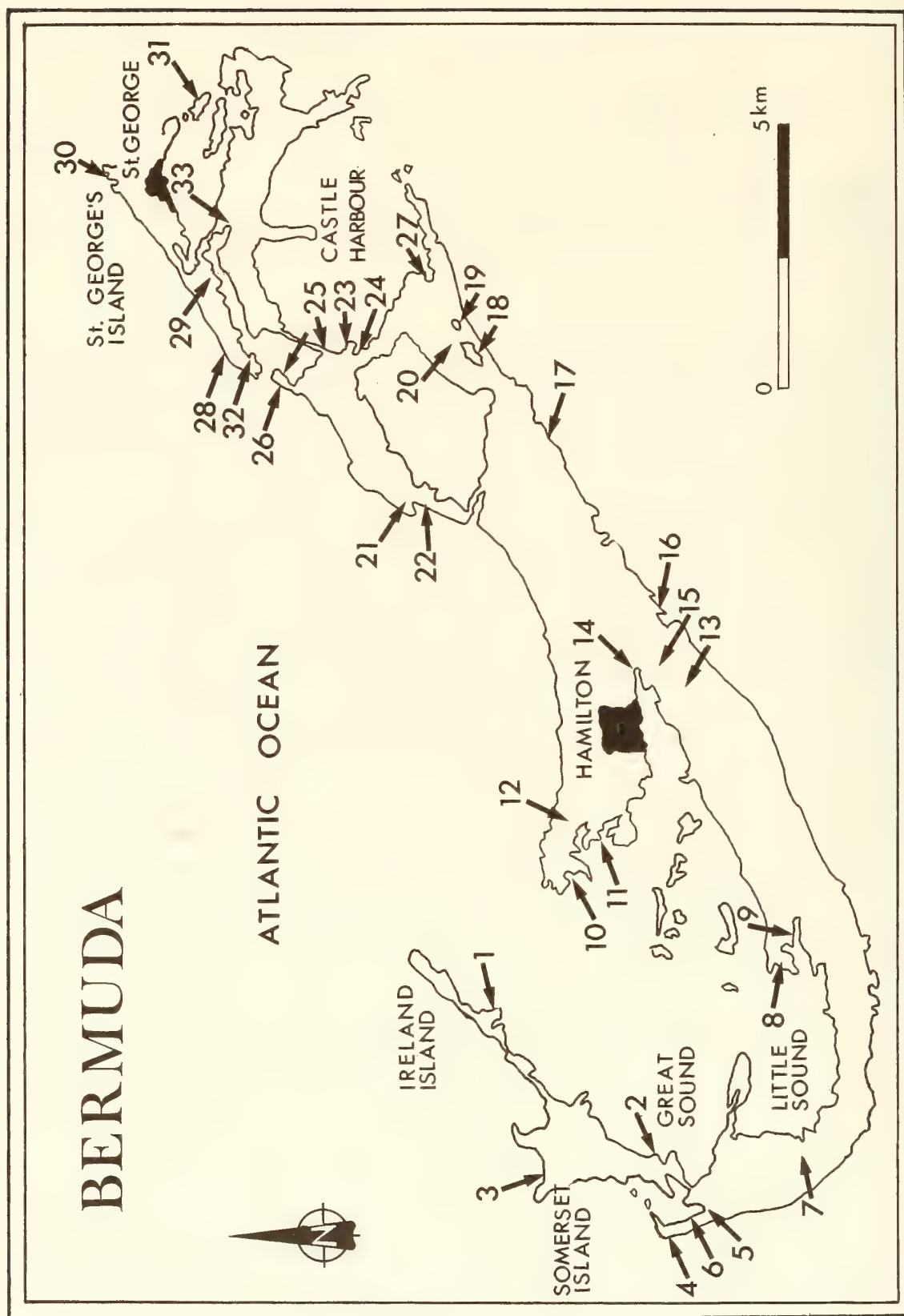


Figure 1. The Bermuda Islands showing the locations of the mangrove swamps surveyed. For locality names see Table 1.

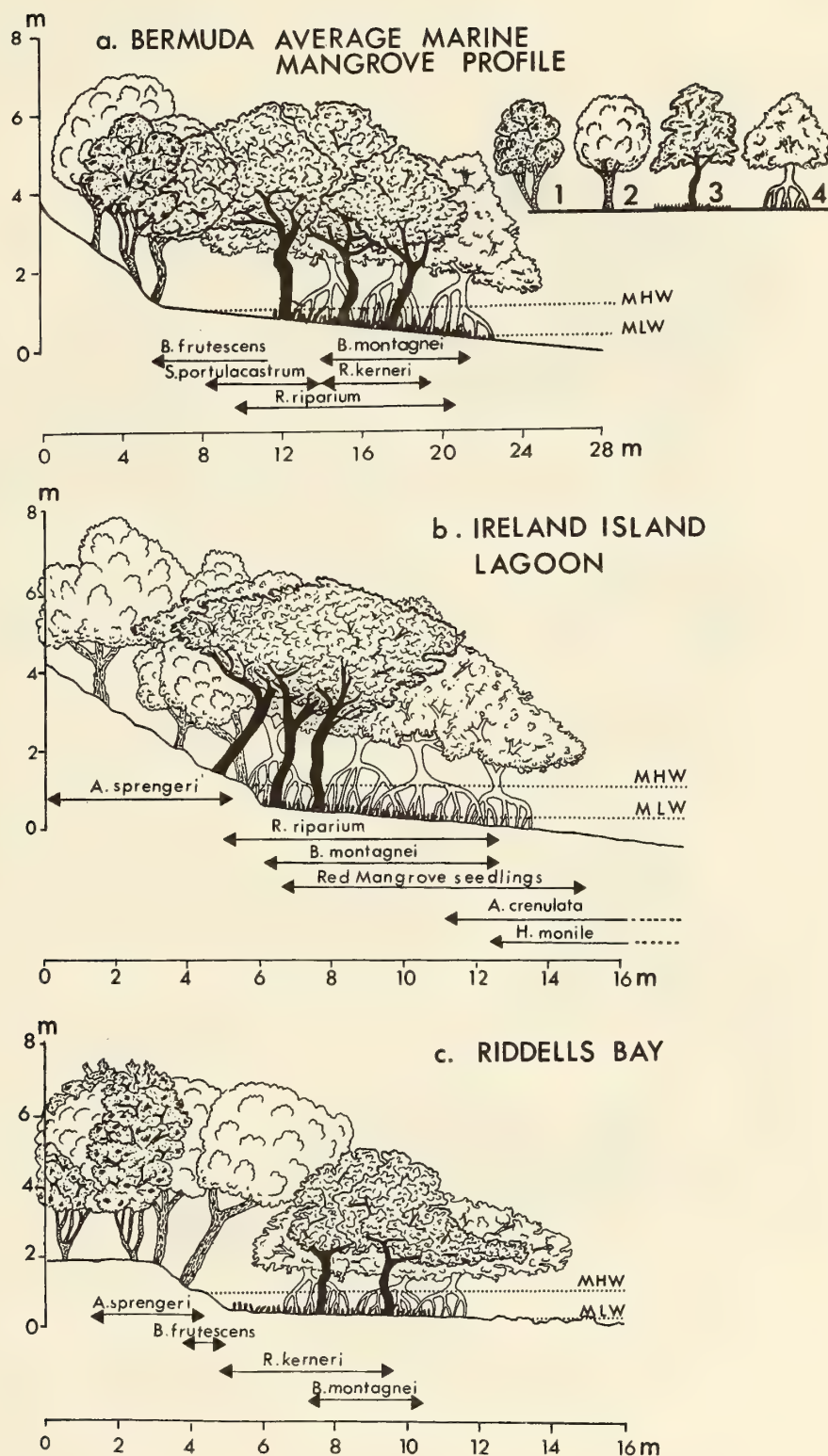


Figure 2. Profiles of Bermudian marine mangrove swamps: 2a, Profile for the average marine mangrove and key. 1=*Schinus terebinthifolia*, 2=*Conocarpus erectus*, 3=*Avicennia germinans*, 4=*Rhizophora mangle*; 2b, Ireland Island Lagoon; and 2c, Riddells Bay.

Species are as in Table 2. MHW = Mean high water. MLW = Mean low water.

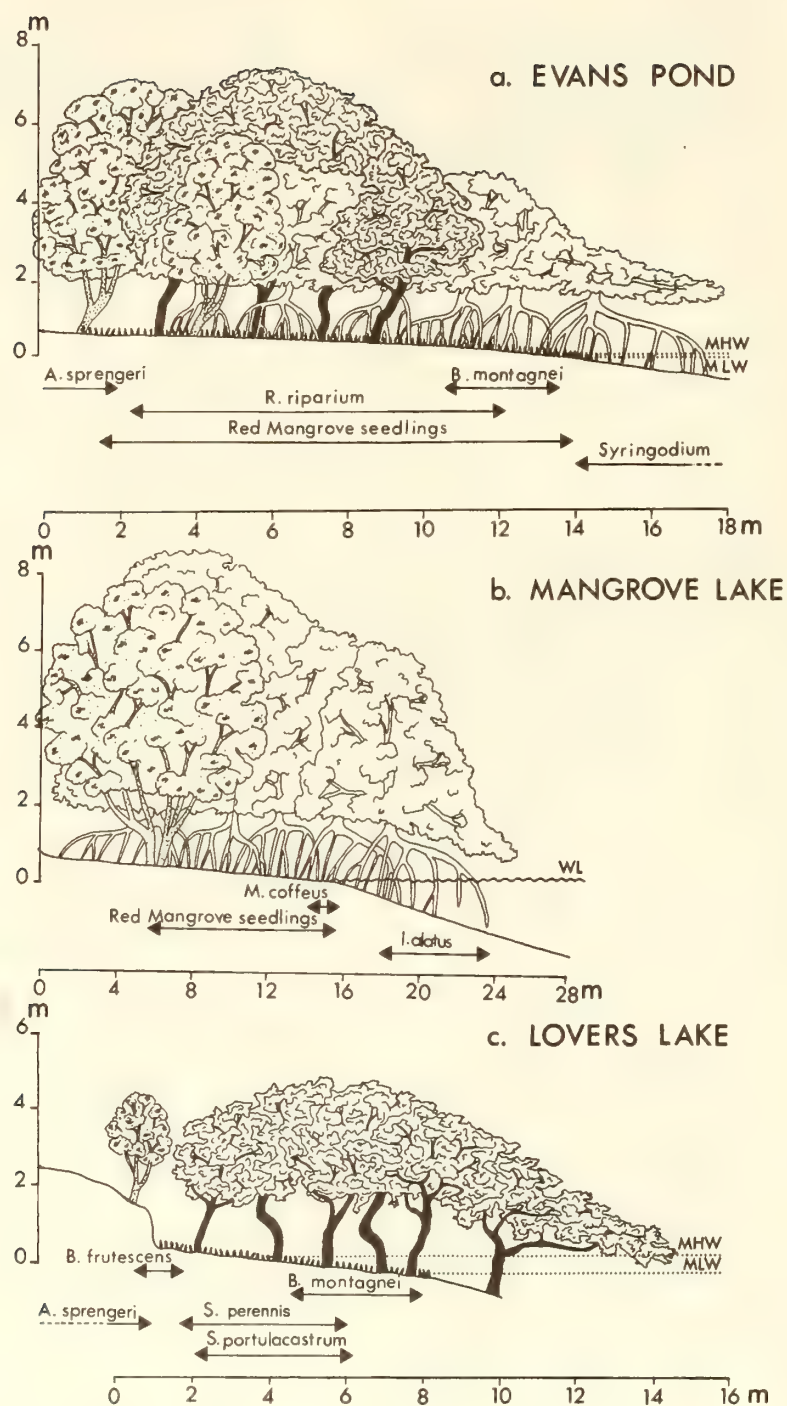
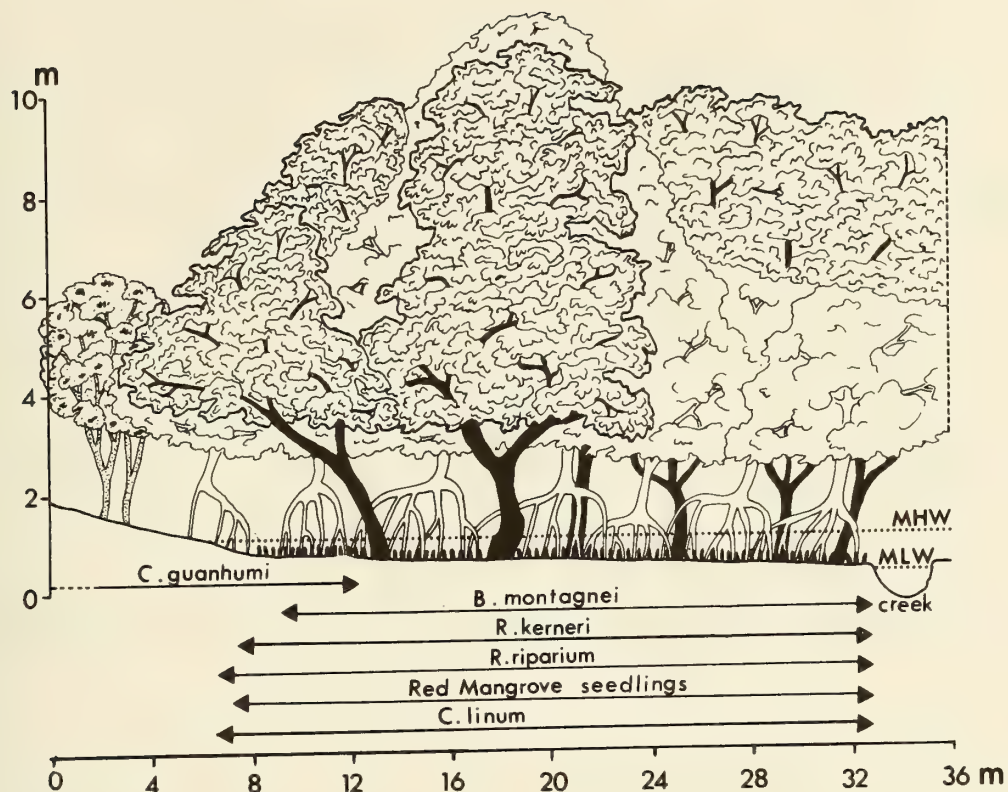


Figure 3. Profiles of Bermudian pond mangroves swamps: 3a, Evans Pond; 3b, Mangrove Lake; and 3c, Lovers Lake. Key and abbreviations as in Figure 2.

a. HUNGRY BAY



b. MILL'S CREEK

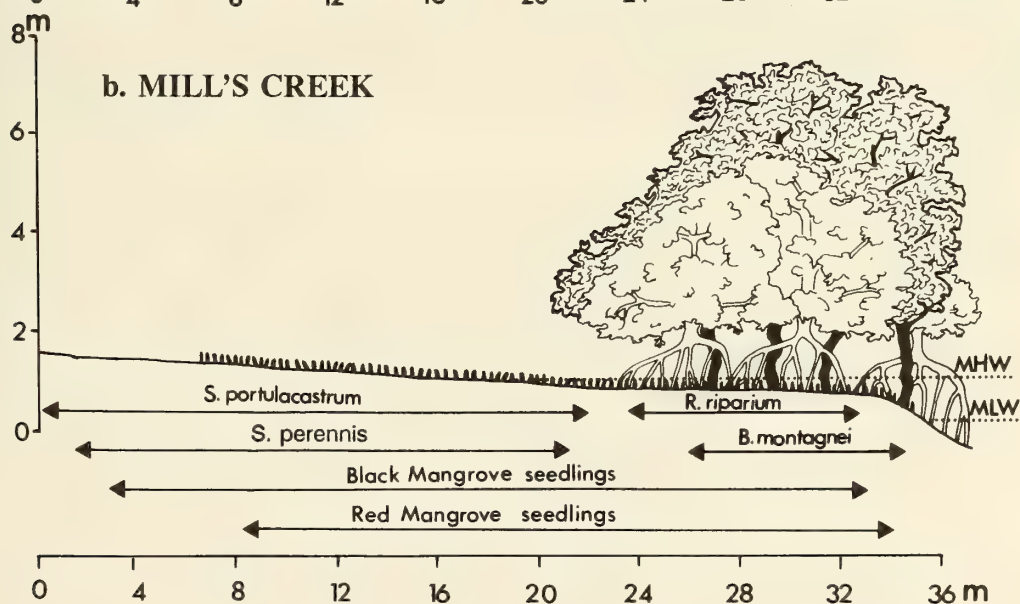


Figure 4. Comparison of two profiles: 4a, Profile of the "Great Mangrove" at Hungry Bay; and 4b, Profile of a mangrove swamp-salt marsh complex at Mill's Creek. Key and abbreviations as in Fig. 2.

About 150 species of macrobiota (Table 1) have been identified from the Bermuda mangroves but only a few species have wide distribution among the mangrove swamps. Seventy-three species (48.7%) were found at a single locality, while only 16 species (10.7%) occurred at 10 or more sites and only four species were present in over 50% of the mangroves. This unexplained discontinuity of distribution generally obscures correlations with obvious physical environmental factors but, the pond mangroves tend to have unique assemblages of associated species. For example, *B. montagnei*, ubiquitous in the bay mangroves, occurs only in the mangrove ponds Walsingham Pond and Lovers Lake. The mangrove oyster, *Isognomon alatus* (Gmelin), and the sponges, *Terpios aurantiaca* Duchassaing & Michelotti and *Chondrilla nucula* Schmidt, occur only in Mangrove Lake and Trotts Pond, the ascidian *Styela plicata* (Lesueur) only in Evans Pond, the holothurian *Synaptula hydriformis* (Lesueur) only in Evans Pond and Lovers Lake, and a host of species, including the endemic *Sargassum bermudae* Grunow, is unique to Walsingham Pond.

In a few locations, mangrove swamps adjoin small salt marshes dominated by *Sesuvium portulacastrum* and/or *Salicornia perennis* Miller with associated *Borrchia arborescens* (L.) A. P. de Candolle. At Mill Creek (Fig. 3b) the salt marsh lies landward of the mangrove whereas at Foot of Crow Lane it fringes the mangrove to the seaward.

The abundance of trees is highly variable among the swamps, the overall mean for *R. mangle* being $3842 \pm 2415 \text{ ha}^{-1}$ and for *A. germinans* $2044 \pm 2200 \text{ ha}^{-1}$. The high standard deviations prevent any correlations with physical or biotic factors.

DISCUSSION

Bay and lagoonal mangrove swamps in Bermuda, although they are smaller, are structurally and floristically similar to those of Florida (Davis 1940, Lugo and Snedaker 1975, Ball 1980), except that overall plant diversity is lower, a situation normal in oceanic islands where opportunities of immigration and colonisation are reduced (Mac Arthur and Wilson 1967). Lot-Helgueras *et al.* (1975) have described floristic characteristics of mangroves at their northern limit in the Gulf of Mexico, a situation comparable to Bermuda, except for latitude and the significant rainfall change within the transitional belt in Mexico. In the Gulf of Mexico, *A. germinans* extends furthest north to 27.3°N, followed by *C. erectus* to 25.7°N; *R. mangle* and *L. racemosa* both stop at about 24°N, however, north of about 23°N, *R. mangle* trees are stunted and poorly developed; at this latitude the floristic composition of the swamp and tree size is similar to Bermuda, except that *Batis maritima* L., very common in the Gulf of Mexico, is absent in Bermuda. South of this latitude in the Gulf of Mexico the mangrove swamps have many more plant species than in Bermuda (Lot-Helgueras *et al.* 1975).

Monospecific stands of either *A. germinans* or *R. mangle* are common in Bermudian pond mangroves at different locations (Table 1). All the Bermudian ponds are relatively close to the sea and the anchialine ones are very close, thus

opportunities for colonisation via the sea may not differ greatly among the ponds. It might be expected that the smaller propagules of *A. germinans* would be transported overland more readily than the larger ones of *R. mangle*, however, several of the more inland swamps such as Mangroville, Paget Marsh and Compston Pond, are colonised by *R. mangle*, while only one, Commonland Marsh supports *A. germinans*. Three of the anchialine ponds have large connections to the sea through which propagules could pass. Of these, Lovers Lake has a monospecific black mangrove stand, Evans Pond supports a community strongly dominated by black mangroves, and Walsingham Pond is principally a red mangrove forest with a few black mangroves. There is no evidence that the presence of either species is related to tidal range or salinity. Both red and black mangroves appear to be equally capable of colonising marine ponds, however, once either alone is established, it appears to be able to occupy the entire zone colonised by both species in Bermudian bay mangroves, resulting in the essentially monospecific stands in inland mangroves. Even where the black mangrove has become established, either through man-made connections as in Paget Island, human introduction as in Evans Pond or natural processes as in Walsingham Pond, typical zonation never develops and the red mangrove characteristically exists as scattered trees or in small clumps.

The times of colonisation of the Bermuda ponds by mangroves are not known, most were basically as they are now when the first settlers arrived (Lefroy 1884), however, Paget Island pond was connected to the sea about 1950 and red mangrove embryos were introduced into Evans pond in the 1970's (D. Wingate *pers. com.*). In the latter case, it is likely that there were a few red mangroves present prior to the introduction since the examination of a few old trunks showed greatly in excess of 20 annual rings, however, a noticeable increase in red mangrove abundance has occurred near to the introduction site but not elsewhere.

The high overall, but low site, total species diversity in the Bermudian mangroves is difficult to explain. Opportunities for colonisation in all but a few isolated inland stands appear not to differ greatly. It seems probable that environmental differences between sites may result in differential rates of settlement, mortality and growth. Some species may have had their distributions reduced by coastal pollution, since it is known that this has happened in the case of *I. alatus*, the mangrove oyster, formerly common in coastal mangroves (Sterreri 1986).

There is no evidence of active succession in Bermudian mangroves most are remarkably stable, reductions being mainly attributable to man's activities. *Schinus terebinthifolia*, a fairly recent introduction is invading the drier, landward fringe of the mangroves. Ball (1980), in studying secondary succession, found long-term stability in Florida mangroves. In fact active succession in mangroves is mostly confined to areas of active sediment accretion (e.g., Davis 1940, Chapman 1944, 1977). West's (1977) observation that there is such great variation in zonation patterns that they do not form a good model for succession, is borne out in the Bermudian mangroves. Mangrove tree abundances are very similar to those cited for Florida by Lugo and Snedaker (1975).

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ATOLL RESEARCH BULLETIN

NO. 387

**DISTRIBUTIONAL CONTROL OF SEAGRASSES BY LIGHT AVAILABILITY,
TWIN CAYS, BELIZE, CENTRAL AMERICA**

BY

J.A. CALEM AND J.W. PIERCE

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DISTRIBUTIONAL CONTROL OF SEAGRASSES BY LIGHT AVAILABILITY, TWIN CAYS, BELIZE, CENTRAL AMERICA

BY

J.A. CALEM¹ AND J.W. PIERCE²

ABSTRACT

Twin Cays are two mangrove islands in the lagoon behind the barrier reef of Belize, Central America with radically different aquatic environments in close juxtaposition. These environments range from open lagoon, with very clear water, to channels with high turbidity, and to creeks immediately adjacent to the mangrove swamps with reddish-brown water. Thirty-eight measurements of beam transmission of blue and green light were made at 11 stations in the channels and creeks of Twin Cays and a few at 2 stations in the open lagoon. Seagrasses, primarily Thalassia testudinum, occur only where blue wavelengths of light can penetrate to the bottom. Loss of blue light is due to either absorption by tannin or backscattering out of the water by suspended particles. Seagrasses are absent in the upper reaches of the tributary channels and creeks because the reddish-brown water, emanating from the mangrove swamps, effectively absorbs blue light. Such plants also are absent from areas that have high turbidity, resulting in scattering of the light and reflection back out of the water. This high turbidity is the result of high concentrations of suspended mineral particles, transported into the major channel between the islands by wind drift, after resuspension of bottom sediments by waves in the main lagoon. Elsewhere, seagrasses are common in Main Channel and lower reaches of the tributary channels.

INTRODUCTION

The type and density distribution of seagrasses in the subquatic environments of the Twin Cays area of Belize vary considerably from place to place. The factors controlling the distribution of this vegetation are not readily apparent in some of the areas. Four things are important and necessary for plant growth: energy from solar radiation, carbon in the form of CO_2 or HCO_3^- , mineral nutrients, and water (Kirk, 1983). Changes in salinity could exert some control on type and density of growth in small areas subjected to extreme runoff after heavy rains. It is doubtful that carbon or

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mineral nutrients are limiting factors, considering the small size of the area and the efficient tidal mixing of the waters. This reconnaissance project is an attempt to determine if the lack of certain wavelengths of light might be a controlling factor for the distribution of some of the seagrasses in the channels and the reason for the deficiency.

Twin Cays is a remnant Pleistocene high (Shinn et al, 1982), lying in the lagoon between the barrier reef and the mainland of Belize, Central America (Fig. 1). Twin

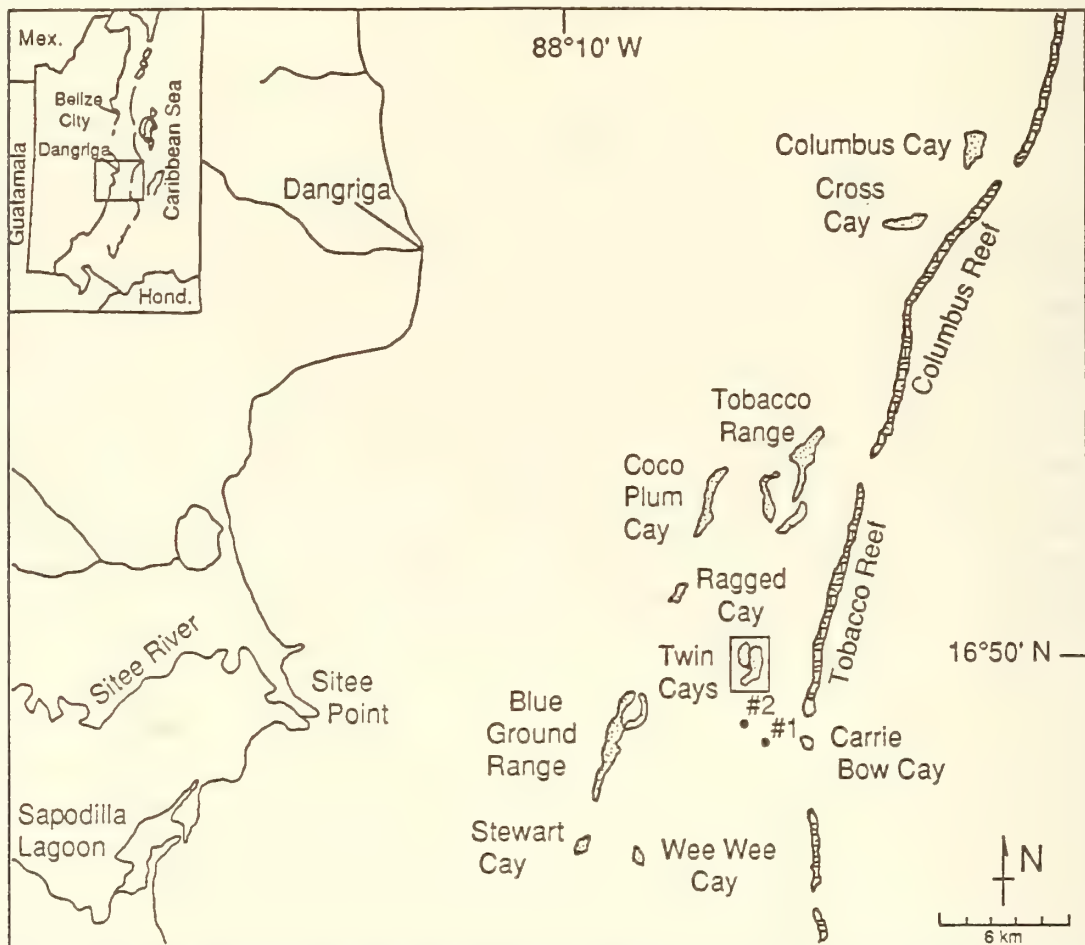


Figure 1. Location map of Twin Cays and location of stations 1 and 2 in lagoon. Outlined area shown in detail in Figure 2.

Cays is approximately 2 km west of the barrier reef and 20 km east of the mainland. Twin Cays consists of two mangrove islands, East and West Islands, separated longitudinally by Main Channel, the major outlet from the mangrove swamps to the deeper lagoonal waters. (Fig. 2). The islands have a land area of 1.8 km². Maximum depth of Main Channel is about 2.5 m, with extensive shoals existing around the margins. Both islands are cut by a complex network of shallow channels draining standing ponds and the densely vegetated mangrove swamps.

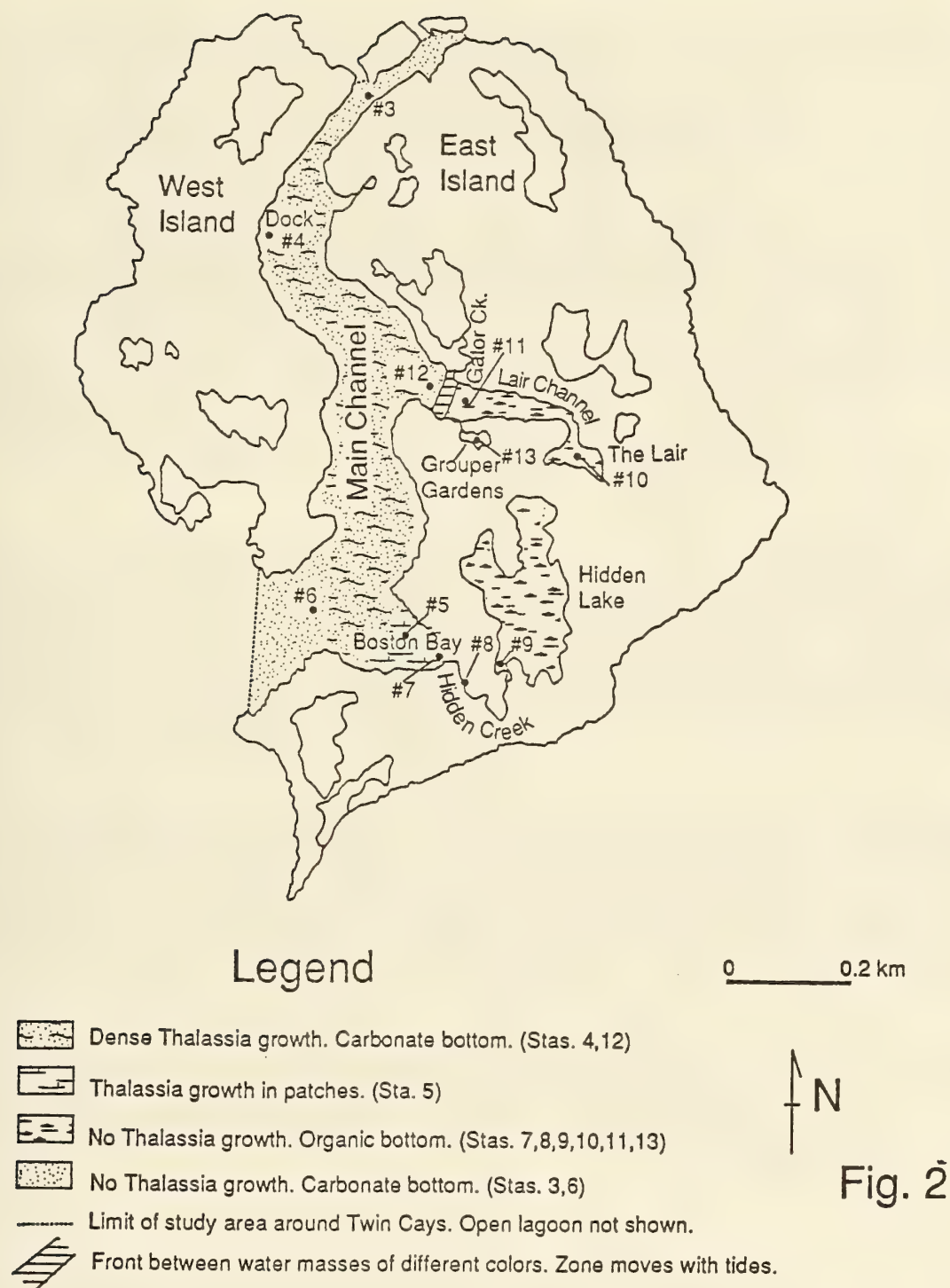


Figure 2. Map of Twin Cays showing location of stations 3 through 13, named features in area, and bottom types.

The region has two seasons, a dry season from November through May and a wet season the remainder of the year with a few weeks transition between the two

(Rützler and Ferraris, 1982). Rain falls nearly every day during the wet season resulting in considerable fresh water runoff from the mangrove swamps.

Dramatic changes in water color and type of material on the bottoms of the channels occur in the Twin Cays area. Water in Main Channel is milky, greenish-blue, often transparent enough to see to the channel bottom. The channel bottom consists of white carbonate sediments. Seagrasses (primarily Thalassia testudinum) grow in profusion over much of the channel bottom except at the north and south ends. Here, the channel floor is bare carbonate sand, sparsely littered with mangrove leaves. Currents associated with north winds carry fine carbonate sediments from shoals, just north of the channel mouth, into the north end of the channel. During these times, the water is highly turbid and it is impossible to see the bottom. A similar situation occurs at the south end of the channel with material swept off the shoals at the south end of East Island by either by refraction of waves around the point, during northerly winds, or as a result of waves generated by southerly winds.

In the creeks and narrow tributary channels, the color of the water changes to deep reddish-brown, colored by tannin leached from the mangrove swamps. The change is abrupt in Lair Channel, occurring over a horizontal distance of less than 2 m, whereas in Boston Bay the change is more gradual, occurring over a distance of 10 m or more. The bottoms of the tributary channels consist of a dark brown organic ooze. Seagrasses grow only in the shallowest parts of these channels, if they are present at all.

Tides, wind velocity and direction, and rainfall greatly affect the water quality in the channels of Twin Cays. Tidal currents scour the floor of the channels when water is funnelled into narrow, shallow channels and creeks. Although relatively well protected from direct winds, a strong current can set up in Main Channel, depending on the strength and direction of the wind. During the times of our sampling, very little resuspended carbonate was transported any great distance into the tributary channels.

Ebb tide moves tannin-charged water from the swamps into the tributary channels. At times of heavy rain there is considerable discharge of fresh water from the swamps such that the tributary channels contain mostly brown water. No brownish water was observed in Main Channel during our sampling, even though several heavy rainstorms occurred.

METHODS

We made trips to Belize in February, 1989 and March, 1990. Both times were during the supposedly "dry" season but in both cases the weather was unseasonably wet, cold, stormy and windy. This reduced the amount of time available for sampling as well as producing unexpected conditions of heavy runoff of fresh water from the mangrove swamps.

Sampling was done at stations in Main Channel and tributaries thereto where water depth was sufficient to operate a small boat (Fig. 2). Two stations in the lagoon, about halfway between Twin Cays and Carrie Bow Cay were also occupied (Fig. 1). These two stations provided a base line of clear water against which the data from the stations in the Twin Cays area could be compared.

Stations were occupied in the morning and afternoon each day, weather permitting, to collect light transmission data and water samples. A Martek[™] transmissometer was used to obtain light transmission values over a 1/4-meter horizontal path length; readings were made throughout the water column at 1/2- or 1/4-m intervals from near-surface to near-bottom at each station. Transmission data were converted to attenuation per meter (c/m) by:

$$c/m = 4[-\ln(t)]$$

where t is the decimal fraction of light transmission per quarter-meter path length. The transmissometer was calibrated in air at 86.5% transmission. In 1989, a green filter (Wratten 61, peak transmission 520 nm) was used in the transmissometer. In 1990, we used the green filter early in the sampling but later installed a blue filter (Wratten 47B, peak transmission 430 nm). The transmissometer only allows insertion of one filter at a time so that the two filters could not be used concurrently. Transmission data from 1985, using different equipment, are also available.

Water samples were collected at near-surface and near-bottom depths at most stations every time the stations were occupied. In a few cases integrated samples of the entire water column were collected, primarily at very shallow stations or if the light transmission profile indicated an homogeneous water column. In 1989, replicate water samples were taken at each depth. The water samples were kept on ice until return to the base station, at which time they were filtered through pre-weighed 0.6 μ m (nominal pore diameter) Nucleopore[™] filters. The filters were stored on ice until return to the laboratory in Washington for determination of concentrations of suspended particulates. Concentrations of total suspended material (TSM) were determined gravimetrically; concentrations of mineral suspended material (MSM) were determined by firing the filters at 1000°C, which destroys the filter in addition to the organic fraction, and weighing the remaining material. Concentrations of organic suspended material (OSM) were determined by the difference between TSM and MSM. No equipment was available for salinity measurement or for fluorescence to measure chlorophyll a concentration. We used a visual measure of water color as a rough indicator of dissolved tannin concentration in the water. We have no independent quantitative measure of dissolved tannin concentration. OSM, therefore, is an underestimation of the total concentration of organic compounds in the water, dissolved or particulate, at any station.

RESULTS AND DISCUSSION

Concentrations of suspensates and light attenuation data by sampling station revealed that marked differences in these values occur over relatively short distances in the Twin Cays area (Table 1). Temporal changes also occurred on a relatively short time scale. For example, there were large differences between the open lagoon (stations 1 and 2) where concentrations of suspensates and light attenuation were consistently low, to Main Channel (stations 3, 4 and 6), where concentrations of mineral suspensates were quite high under certain wind conditions and light attenuation varied sympathetically with concentration. In the small creeks and secondary channels

TABLE 1

STA.	YR	TSM	OSM	MSM	BLUE ATTN	GRN ATTN	STA.	YR	TSM	OSM	MSM	BLU ATT	GRN ATT
1	89	0.12	0.00	0.12		0.12	10S	90	0.57	0.32	0.25		0.70
2	89	0.12	0.00	0.12		0.00	10B	90	2.99	0.64	2.35		0.72
6S	89	0.62	0.16	0.46		0.47	5S	90	0.57	0.46	0.10		0.29
6B	89	0.86	0.04	0.82		0.68	5B	90	0.40	0.22	0.19		0.08
7	89	1.09	0.64	0.45		1.07	13	90	0.59	0.35	0.24		0.42
9	89	1.14	0.67	0.47		1.58	3S	90	0.43	0.36	0.07	0.00	
13	89	0.18	0.00	0.18		0.75	3B	90	1.40	0.54	0.86	0.17	
3S	89	1.04	0.73	0.31		1.26	4	90	0.71	0.25	0.46	0.17	
3B	89	2.08	0.84	1.24		1.60	12	90	2.36	1.39	0.96	0.88	
4	89	0.87	0.55	0.32		0.84	11S	90	0.24	0.00	0.24	0.54	
3S	89	0.99	0.23	0.76		0.51	11B	90	0.60	0.18	0.42	0.37	
3B	89	1.55	0.55	1.00		1.54	10S	90	1.83	1.80	0.03	3.70	
4	89	0.66	0.00	0.66		0.70	10B	90	1.31	1.31	0.00	1.59	
11S	89	0.57	0.16	0.41		1.10	7S	90	0.71	0.64	0.07	1.97	
11B	89	0.58	0.33	0.25		0.88	7B	90	1.59	0.85	0.74	1.24	
12	89	0.76	0.07	0.70		1.05	6S	90	0.42	0.07	0.35	0.95	
3S	90	0.97	0.41	0.55		0.65	6B	90	0.76	0.52	0.24	1.29	
3B	90	1.07	0.55	0.52		0.65	13	90	2.7	2.42	0.29	1.42	
11S	90	0.84	0.40	0.44		0.65	8S	90	1.24	0.99	0.25	1.94	
11B	90	0.79	0.25	0.54		0.75	8B	90	0.71	0.35	0.36	1.14	

	TSM	OSM	MSM	BLUE ATT	GRN ATT
AVE	0.96	0.51	0.47	1.16	0.76
STD	0.65	0.50	0.42	0.91	0.43
N	40	40	40	15	25
MAX	2.99	2.42	2.35	3.70	1.60
MIN	0.12	0.00	0.00	0.00	0.00

Table 1. Concentrations of total, organic, and mineral suspensates (mg/l) in samples and blue and green attenuation values (c/m) for 1989 and 1990 readings. S and D after station numbers indicate near-surface (S) and near-bottom (D) samples.

of the mangrove swamps, high concentrations of organic material were found and blue light was more highly attenuated than green light.

Beam attenuation of selected wavelengths of light is dependent upon absorption by the water as well as upon absorption and scattering by constituents, either dissolved

or suspended, in the water. Since scattering is generally not wavelength sensitive, except when highly colored particles are present (Jerlov, 1976), blue and green wavelengths should be equally affected by scattering. Absorption is wave length dependent. Therefore, we assume that, if the green and blue wave lengths were similarly affected under the same conditions, scattering predominated.

Least squares regression analysis (outliers dropped) reveals that attenuation of green light is significantly correlated with TSM at the .999 confidence level (Fig. 3), as well as with the concentrations of MSM and OSM at the same confidence level. Attenuation of blue light, on the other hand, is correlated only with the concentration of OSM at a .997 confidence level (Fig. 4), and is not significantly correlated with either the concentration of TSM or MSM. This suggests that the dominant cause of blue light attenuation is absorption by organic material, not scattering. Dissolved organic

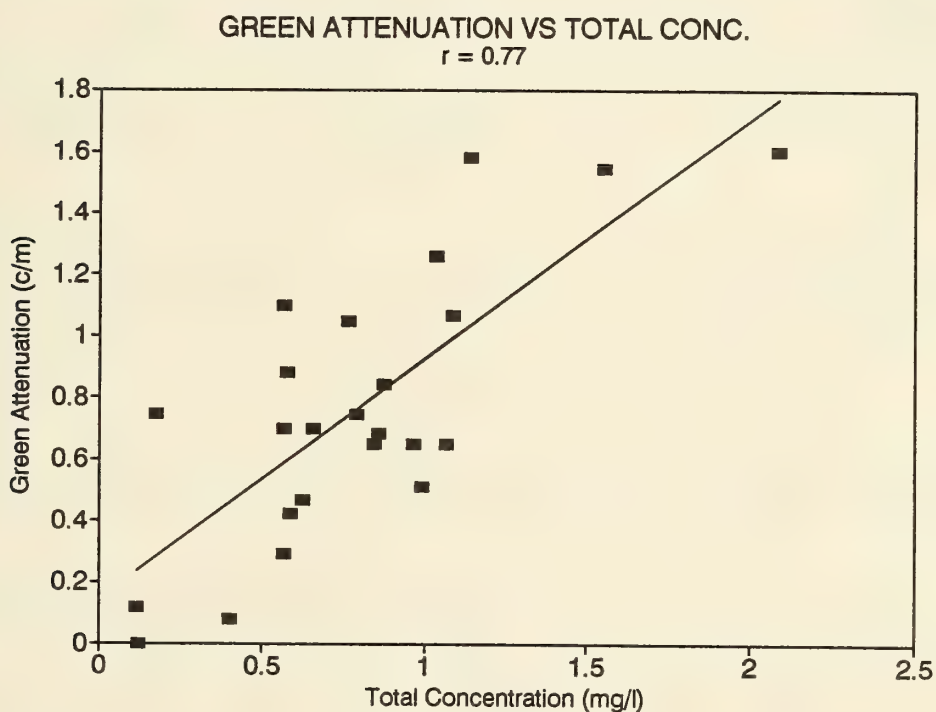


Figure 3. Plot of green attenuation (c/m) versus TSM concentration (mg/l). $r=0.77$. One outlier not included in plot.

material, giving rise to the reddish-brown coloration in the water, plays an important part in the absorption process by selectively absorbing the blue wavelengths of light. Interestingly, concentrations of organic and mineral suspensates are not significantly correlated with each other. This indicates that the organic and mineral phases of suspended particulates are derived from different sources; i.e., organic suspensates from the mangrove swamps and mineral suspensates from the Main Channel and fringing shoals.

Interestingly, concentrations of organic and mineral suspensates are not significantly correlated with each other. This indicates that the organic and mineral phases of suspended particulates are derived from different sources; i.e., organic suspensates from the mangrove swamps and mineral suspensates from the Main Channel and fringing shoals.

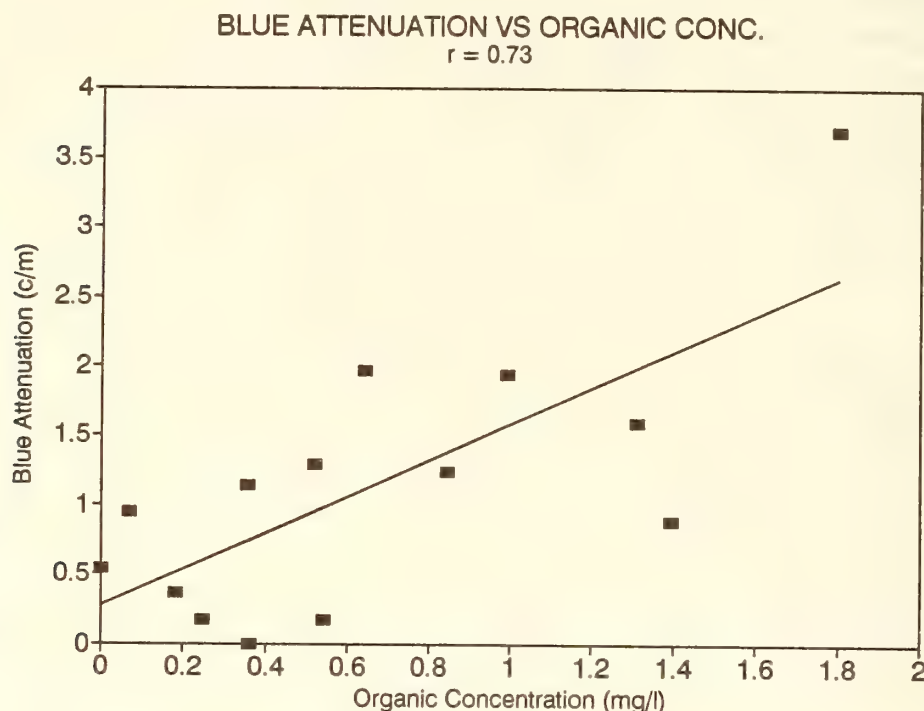


Figure 4. Plot of blue attenuation (c/m) versus concentration of OSM. $r=0.73$. One outlier not included in plot.

A nonlinear regression model of green light attenuation and TSM results in a better fit than a linear relationship. We fit $c/m = b_1 \exp(-b_2/x)$ where c/m is the attenuation per meter path length, the b 's are constants and x is TSM. R^2 , the proportion of the variance of the dependent variable explained by this regression, is 0.88 ($r=0.94$) as opposed to 0.59 ($r=0.77$) for the linear regression. Such a model implies that there is a limiting value of TSM for green light attenuation; i.e., above this critical value of TSM, no further change occurs, to any great degree, in green attenuation.

Water in the open lagoon (stations 1 and 2) attenuated very little light of either wavelength. Blue and green attenuation for these stations were approximately equal (1985 data). Concentrations of OSM were below detection level and concentrations of MSM were the lowest recorded in the study area. These waters, within the limits of the Martek transmissometer and assuming very little particle scattering, are similar to extremely clear oceanic waters (Smith and Baker, 1981).

Concentrations of suspensates and beam attenuation in the enclosed waters of Twin Cays were quite variable. Concentrations of MSM were highest in Main Channel. Concentrations of OSM were highest in the tributary channels and creeks. MSM contributed only a negligible amount of material to the total suspended load at the stations in the channels and creeks.

Scattering predominated over absorption through most of Main Channel (stations 3 & 4). Blue attenuation was consistently low at these stations and slightly less than green attenuation. Differences in attenuation occurred at stations in the Main Channel but appear to be due to changes in the concentrations of MSM rather than changes in concentration of OSM. We found little evidence of absorption of blue light over green, indicating that scattering predominated.

When the wind was from the north, the water at the north end of Main Channel (Sta. 3) was milky green because of high concentrations of suspended carbonate particles. Sight distance into the water column was limited. Green light was highly attenuated at this time. When there was no wind, the water at the north end of the Channel was extremely clear. Attenuation of blue light at the north end of the channel under conditions of little to no wind was quite low.

Wind frequencies from the northwest and northeast are quite common in the Twin Cays area (Rützler and Ferraris, 1982). Hence, the northern end of Main Channel must be quite turbid a considerable part of the time. Thalassia growth is extremely sparse in this area.

The water at the dock (Sta. 4) was relatively clear on all occasions we visited Twin Cays. Attenuation of blue light was less than that of green. Average concentrations of OSM was less than that of average concentrations of MSM. Values of attenuation and particulate concentrations at the dock were less than those at the north end of Main Channel. Thalassia is abundant in this area.

Waters in the southern part of Main Channel (Sta. 6) were more turbid than those at the dock at the time of our visits. Average blue attenuation was greater than average green attenuation, suggesting the presence of some dissolved tannin in the water. Concentrations of MSM were greater than those of OSM. Under conditions of a southeasterly or easterly wind, turbidity could become quite high in the southern part of Main Channel. Thalassia growth is sparse, which may be due to greater water depth, significant intermittent turbidity, presence of dissolved organic material, or a combination of factors.

Attenuation of blue light was double that of green in the tributary channels where reddish-brown water was present. The farther up these channels and closer to the influence of the mangrove swamps, the greater was the attenuation of the blue

wavelengths. This is due to an increase in absorption of the shorter wavelengths by the brownish water. OSM concentrations were higher than MSM at these stations.

At Hidden Lake (Sta. 9), Hidden Creek (Sta. 8), and its opening into Boston Bay (Sta. 7), attenuation of blue light was greater than that of green. Absorption predominated over scattering. Attenuation of blue light was higher in the surface waters than the water near the bottom both times that we visited the area in 1990. The high values were due to fresher, tannin-charged waters emanating from the mangrove swamps during ebb tide, a situation similar to that noted by Mazda, et al. (1990).

OSM concentrations were greater than MSM in these reddish-brown waters in the Hidden Creek area. The bottom was composed of a thick brown organic ooze. No Thalassia growth was present. Suspensate concentrations (TSM) were higher in near-bottom waters in one instance and in near-surface waters in the other when we sampled in this area. In the former case, sampling occurred at mid-ebb tide (highest current velocity) and the high suspensate concentration is attributed to resuspension of bottom sediments by tidal currents. In the latter case, sampling occurred near low tide or very early flood tide when would expect the surface water to consist primarily of fresher water from the swamps with any suspensate material that was present originating in the swamps.

The transition from the greenish-blue water of Main Channel to the reddish-brown water flowing from Hidden Creek appeared to be gradual across Boston Bay, suggesting efficient mixing of the two water types. Attenuation of green light was less in Boston Bay (Sta. 5) than at either the southern end of Main Channel (Sta. 6) or at Hidden Creek (Stations 7 and 8). Concentrations of TSM were generally quite low. The low concentration of MSM at the center of Boston Bay would indicate that most of the suspended mineral matter at the southern end of the Main Channel rapidly settled out of the water column in the quieter waters of Boston Bay. The low concentration of OSM here would indicate that the organic-rich waters of Hidden Creek were effectively diluted by mixing with the greater volume of clearer water in the more open Boston Bay. No blue light transmission values were taken in this area. Thalassia grows in patches in this area, the density of growth declining toward Hidden Creek.

A distinct front between brown and green water masses existed in Lair Channel at the times of sampling. The change in appearance of the water color across the front was dramatic. Up channel, the water was reddish-brown; down channel, a milky green. The front moved up and down channel in response to tidal stage. Seagrass growth was dense down channel whereas it rapidly disappeared up channel and by the Lair (Sta. 10), no seagrasses were present. There was no difference in attenuation of green light in the two types of water in 1989. Attenuation of green light in the reddish-brown water in 1990 was similar to that of 1989. We expected that there would be a marked difference in attenuation of blue light in the different water masses revealing a difference in tannin enrichment across the front, i.e., the brown water having higher

blue attenuation values than the green water. In fact, higher blue attenuation occurred down channel in the green water than up channel in the brown. Offsetting the possible greater absorption by the brown water, concentrations of suspensates (TSM) were nearly an order of magnitude higher in surface waters on the green water side of the front at the time of sampling. Substantial scattering of blue light may account for the high value of blue light attenuation. Toward the Lair (Sta. 10), which dead-ends at the mangrove prop roots, the attenuation of blue light increased to where less than 8% of the incident light was transmitted over a distance of one meter.

Grouper Gardens (Sta. 13) presents an interesting case. Although this small inlet is surrounded by mangrove swamps, the water appears to be relatively clear and has a greenish brown coloration. The bottom is covered with the green alga, Avrainvillea sp. No seagrass is present in this inlet although the water clarity would suggest that such plant growth could be supported. Attenuation of the blue wave lengths of light was greater than that of the green wave lengths, indicating a considerable amount of tannin in the water. The apparent clarity of the water may have been deceptive because of a relatively shallow depth of this inlet. The exclusion of Thalassia from this area may be accounted for by a lack of blue light or intense grazing pressure in these dense stands. Avrainvillea sp. produces secondary metabolites, which are not palatable to grazing fish, thus reducing herbivory (J. Norris, pers. comm.).

Large aggregates, primarily of organic material with included carbonate particles, often appear in the water column in Lair Channel and Grouper Gardens. These aggregates apparently have become detached from the bottom by the positive buoyancy imparted by bubbles within the aggregates. They were most common on bright sunny days in the afternoon and it is assumed that the bubbles were oxygen generated by algae on the bottom. The aggregates, although accounting for a large proportion of the mass of the suspensates and important for mass balance and export studies, had little effect on light transmission. Therefore, they were deliberately excluded from the water samples taken for concentration data. The aggregates broke apart when attempts were made to obtain samples and display a fragility similar to that reported for marine "snow" (Hammer et al., 1975).

CONCLUSIONS

Transmission of light controls the distribution of seagrasses in the Twin Cays area of the Belize lagoon. The absence of Thalassia in areas of highly colored water and in areas of high concentrations of suspensates strongly suggests that this is the case.

Tannin, either dissolved or particulate, strongly absorbs blue light. In highly-colored, reddish-brown waters, where it is presumed that high concentrations of dissolved tannin were present, very little blue light penetrates more than a few centimeters into the water. Apparently, the amount of tannin is critical to whether any seagrasses are thriving or even present. It seems that very little tannin need be present

to exclude Thalassia from an area, as shown by its rapid disappearance in Lair Channel over a relatively short distance.

Suspended mineral grains contribute to beam attenuation by scattering. Very high concentrations cause such an increase in scattering that little, if any, solar radiation would be available to seagrasses in such areas. Such situations occur at the north and south ends of Main Channel where a considerable amount of the incident light is backscattered out of the water. Two alternative explanations might account for the lack of plants at the two ends of Main Channel. First, sedimentation rates could be high enough to smother any new Thalassia growth in the area. Second, currents set up through the channel by wind drift could possibly prevent colonization of the area by any rooted aquatics. The presence of mangrove leaves exposed on the bottom of the channel suggests that the rate of sedimentation is not very high in this area. The mangrove leaves also indicate that the currents are not of sufficient strength to move the leaves out of the area and, hence, probably not of sufficient strength to prevent rooting of Thalassia. Thus, we assume that sufficient amount of radiation is removed from the incident solar radiation, during passage through the water column by backscattering, that there is an insufficient amount necessary for plant growth.

Tides cause significant short-term variations in water quality at Hidden Creek and its environs. At ebb tide, organic-rich waters flow from the mangrove swamps. Efficient mixing with waters from Main Channel occurred in the area of Boston Bay. This embayment, connecting Main Channel with Hidden Creek, showed evidence of mixing of swamp and lagoonal water masses. Concentrations of mineral suspended matter in Boston Bay were lower than those in Main Channel while concentrations of organic suspended matter were intermediate between those at Main Channel and Hidden Creek. In Lair Channel, less mixing of tributary and Main Channel waters was evident. There was a distinct line between water masses of different colors. Down channel, the water shared characteristics with waters of Main Channel and was milky bluish-green. Up channel, the water was reddish-brown, revealing its source to be the swamps. The large difference in light transmission up channel and down channel becomes especially apparent at the Lair.

ACKNOWLEDGMENTS

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ATOLL RESEARCH BULLETIN

NO. 388

**SOME REEFS AND CORALS OF ROATAN (HONDURAS), CAYMAN BRAC,
AND LITTLE CAYMAN**

BY

DOUGLAS P. FENNER

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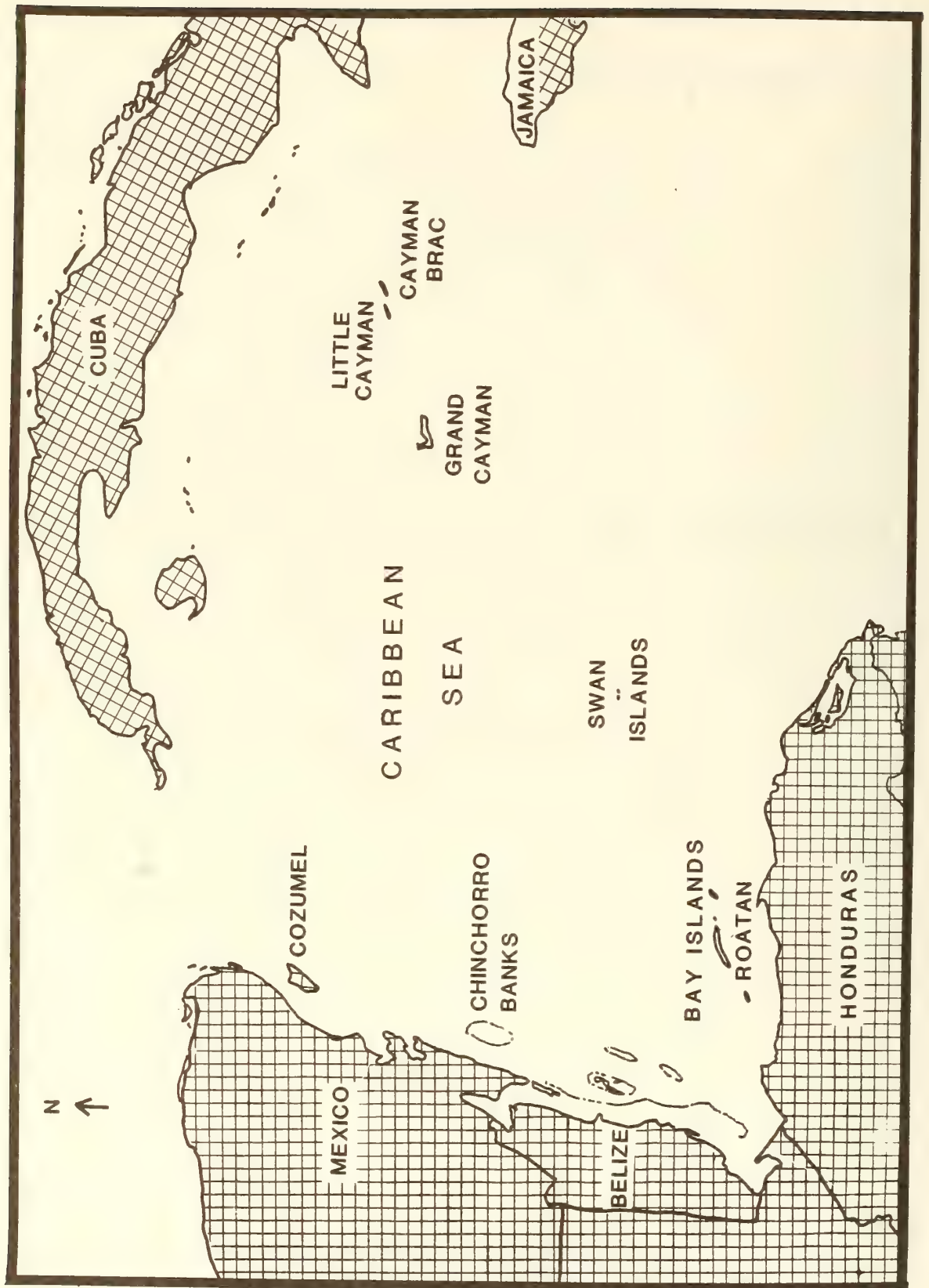


Figure 1. Map of the western Caribbean, showing island locations.

SOME REEFS AND CORALS OF ROATAN (HONDURAS), CAYMAN BRAC, AND LITTLE CAYMAN

BY

DOUGLAS P. FENNER

Abstract

The topography, zonation, and coral communities of small sections of the reefs which surround three western Caribbean islands were studied for comparison with well-studied Caribbean reefs. The reefs of northwestern Roatan (Honduras), southwestern Cayman Brac, and northwestern Little Cayman all have terraces at 5-10 m depth and 15-20 m depth, and a nearly vertical deep forereef, with the exception of one section on Little Cayman which lacks the deep terrace, and sections on Roatan that have only one terrace. Northwestern Roatan has a well-developed set of buttresses and sand channels, although it receives little wave energy. Forty-four taxa of corals were found on Roatan, 47 on Cayman Brac, and 45 on Little Cayman. Nine were new records on Roatan, 24 were new on Cayman Brac, and 20 on Little Cayman. The Shannon-Weaver diversity index averaged 1.38 over a 0.1-15 m depth range at Roatan, and 1.58 over 0.1-25 m depth at Cayman Brac, indicating slightly low and average coral diversities compared to other Caribbean reefs. Coral cover averaged 21% at Roatan and 20% at Cayman Brac, indicating a slightly low coral cover for Caribbean reefs, well within the range reported.

INTRODUCTION

At one time, Caribbean coral reefs were considered to have much less abundant and diverse life than Indo-Pacific reefs (Wells, 1988). Intensive study by many investigators at a few Caribbean sites (such as Discovery Bay, Jamaica, and Carrie Bow Cay, Belize) has revealed a surprising abundance and diversity of organisms (e.g., Wells and Lang, 1973; Liddel and Ohlhorst, 1989; Rutzler and Macintyre, 1982a). One group, the sponges, has been found to be as diverse and have greater biomass in the Caribbean than in the western Pacific (Wilkinson, 1988). Only by the study of additional reefs will it become clear whether the faunas of well-studied reefs are unusually abundant and diverse, or representative of other reefs. In addition, our understanding of the topography and zonation of Caribbean reefs is derived from a limited number of well-studied reefs, and may benefit from the study of additional reefs.

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Roatan (Honduras), Cayman Brac, and Little Cayman are three small islands of the western Caribbean surrounded by coral reefs that have received limited quantitative study (Wells, 1988). The Bay Islands of Honduras (Utila, Roatan, and Guanaja) have well-developed reefs that support a small diving industry (Halas and Jaap, 1982; Wells, 1988). The reefs of Roatan have been surveyed in an unpublished study by Halas and Jaap (1982), who found 47 taxa of stony corals. Numbers of coral taxa are adjusted here to be consistent with Wells and Lang (1973) as modified by Cairns (1982). The first part of the present study concentrates on the protected reefs of northwestern Roatan. Burke (1982) reported that the Belize Barrier Reef is best developed where it is protected from waves by 3 atolls, and Fenner (1988) and Jordan (1988) reported better developed reefs on Cozumel's leeward side than the small reefs briefly studied on its windward side (Boyd et al., 1963; Jordan, 1989). Yet in the same area, the windward reefs of three Belize atolls (Stoddart, 1962) and Banco Chinchorro (Jordan and Martin, 1987) show at least as much development as their leeward reefs. The best developed reefs of Belize, Mexico, and Grand Cayman are not subjected to siltation stress (Burke, 1982; Fenner, 1988; Roberts, 1974). The Bay Islands are high islands which, although small, may release significant amounts of sediments onto surrounding reefs (Halas and Jaap, 1982). The first part of this study describes the protected reefs of northwest Roatan (Honduras) with quantitative reef profiles and coral population studies.

The Cayman Islands are three limestone islands surrounded by coral reefs (Wells, 1988). The coral reefs of Grand Cayman have been described in detail (Roberts, 1971; Roberts, 1974; Raymont et al., 1976; Rigby and Roberts, 1976; Roberts, 1977; Roberts, in press). Cave-dwelling invertebrates of Grand Cayman have also been described (Logan, 1977; 1981), as well as some boring sponge populations (Rose and Risk, 1985) and coral bleaching (Ghiold and Smith, 1990). Fifty-six species of corals have been reported from Grand Cayman (Roberts, in press; Logan, 1981; Fenner, unpublished report of *Thalamophyllia riisei*). Reefs of Cayman Brac and Little Cayman have been described and mapped by Logan (1988; in press). The topography and zonation of the reefs of Cayman Brac and Little Cayman are similar to those at Grand Cayman in most places (Rigby and Roberts, 1976; Roberts, 1977; Logan, in press; Roberts, in press). Most of Cayman Brac is surrounded by a fringing reef with no lagoon, but a shallow lagoon is present along a small section of southwestern Cayman Brac. Most of Little Cayman is surrounded by a fringing reef, enclosing a shallow lagoon (Logan, in press). The reefs around both islands have two terraces separated by a small, coral-covered escarpment. In the Bloody Bay area of northwestern Little Cayman, the lower terrace is absent; a near-vertical wall

begins in as little as 7 m depth. In the second segment of this study, quantitative reef profiles and coral population studies of small sections of southwestern Cayman Brac and northwestern Little Cayman (Bloody Bay) are reported.

ISLAND DESCRIPTION

Roatan (Honduras), Cayman Brac, and Little Cayman are all relatively long, thin islands oriented in a nearly east-west direction, located in the western Caribbean (Fig. 1). The island of Roatan and surrounding submarine areas are described elsewhere (Banks and Richards, 1969; McBirney and Bass, 1969; Davidson, 1974; Wilensky, 1979; Halas and Jaap, 1982; Wells, 1988). Cayman Brac and Little Cayman have also been described (Stoddart and Giglioli, 1980; Wells, 1988; Logan, in press). Roatan is a hilly island, with little limestone, while all three Cayman islands are low-lying limestone islands. Rainwater runoff is extensive on Roatan, but very limited on the Caymans. Thus, the reefs surrounding Roatan are periodically subjected to siltation during heavy rains (Halas and Jaap, 1982). Rainwater percolates through the porous limestone of the Cayman Islands, removing any silt. Hurricane Allen which greatly damaged Jamaica's north coast in 1980 (Woodley et al., 1981) may have had less effect on Cayman Brac, since it passed by more rapidly. A major hurricane struck Cayman Brac in 1932, taking over 100 lives. Hurricane Gilbert passed over the Caymans on September 13, 1988, after the present study of Cayman Brac, but before the present study of Little Cayman. No damage from Gilbert was found on Little Cayman's northwestern reefs. The reefs of Roatan had no legal protection at the time of this study, and were subject to limited amounts of fishing, coral collecting, sewage, and refuse dumping. All of the reefs in Cayman waters have been legally protected since 1986. The reefs at all sites showed little diver-related damage.

METHODS

Data for this study were gathered from Roatan in April 1987, from Cayman Brac in January 1988, and from Little Cayman in June 1989.

Measurements were made of depth profiles and coral species diversity. Depth profiles were made using a taut 5 m polypropylene line and a depth gauge. The maximum depth of this study was 30 m. Species diversity data were obtained in Roatan by photo belt-quadrats and a visual line transect, and in Cayman Brac by making belt-quadrats with a movable grid. Weinberg (1981) found that photo and grid belt-quadrats were more accurate than line transects. Photo belt-quadrats were made in Roatan by photographing approximately 1 x 0.65 m rectangles of reef from points

directly above the surface of the reef. Coral cover and diversity data were obtained by projecting the photographic slides and approximating the corals as measured rectangles and triangles. The photo belt-quadrats were taken parallel to depth contours (e.g., Bradbury et al., 1987; Wilkinson and Evans, 1989; Cortes, 1990; Gates, 1990), as was the visual line transect (e.g., Loya, 1972; Porter, 1972; Liddell and Ohlhorst, 1987). Belt-quadrats and line transects were placed in different zones or habitats (e.g., Bradbury et al., 1987; Liddell and Ohlhorst, 1987; Cortes, 1990). This design does not allow capturing the zonation between the depths selected. Belt-quadrats were made at 3, 8, and 15 m depth at "Overheat Reef" ($86^{\circ}35'W$, $16^{\circ}19'N$; Fig. 4B) and "Deep Eel Garden" ($86^{\circ}35'W$, $16^{\circ}20'N$; Fig. 4B). These similar-appearing sections of the same reef were marked with mooring buoys attached to the coral rock, and separated by about 1 km. Dive site names are those used by local dive operators and which appear in the popular dive press. The number of photos taken at each location is indicated in Table 2. Species-area curves began to level out after 10-15 quadrats (Fig. 2), requiring the combination of the two belt-quadrats at each depth. The number of colonies was not counted, since connections between colonies might be hidden in the photos, making such a count unreliable. A line transect of the reef crest in Roatan was made by laying a taut 5 m length of polypropylene line across the bottom parallel to the shoreline. The line was moved to produce 10 contiguous extensions of the first placement. A ruler was placed on corals to measure the section of line traversing each coral colony; Porter (1972) found parallax problems to be very small. Vertical extensions of colonies and hidden sections of corals were

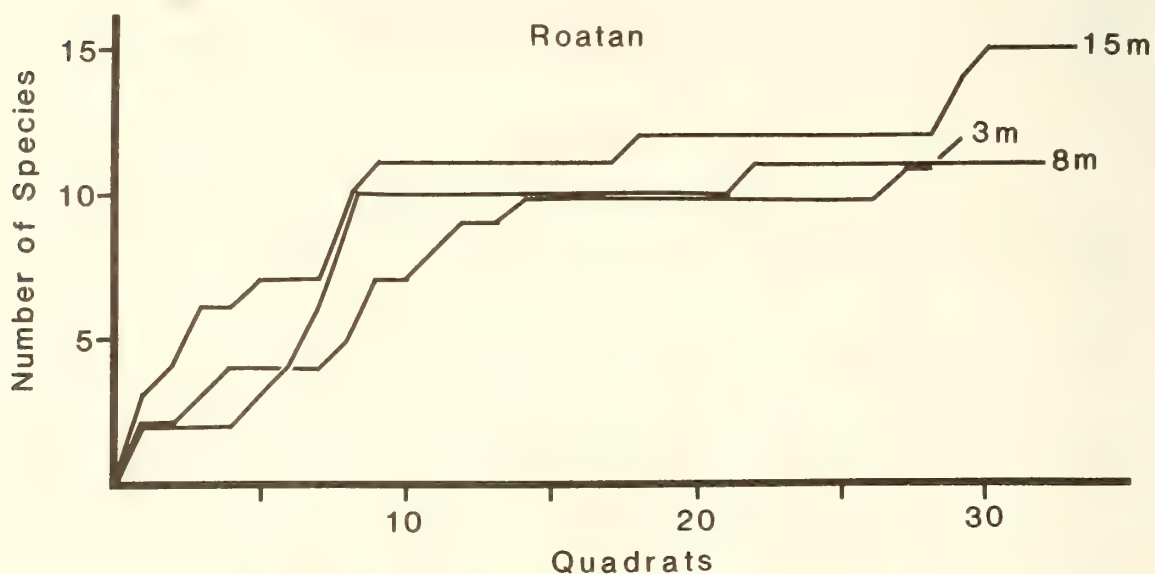


Figure 2. Species-area curves for Roatan.

not included in the measurements, nor were other organisms. A line transect was made on the crest because the water was too shallow to allow a photo transect. The line transect was made in front of Anthony's Key ($86^{\circ}35'W$, $16^{\circ}20'N$; Fig.'s 4B, 5).

The moveable grid used for belt-quadrats on Cayman Brac consisted of a 1 x 1 m frame of PVC tubing divided into 16 equal squares by 6 lines. The grid was placed on the reef, and the coverage of each coral species estimated. Estimates of large corals were made in squares, and small corals in cm^2 . After coral cover estimation, the frame was moved to the adjacent area, in a straight line along the depth contour. Belt-quadrats were made in each of 6 visually identifiable zones which are listed along with the depth and location in Table 3. Reef locations were named and marked with buoys as in Roatan. Two belt-quadrats were made in the terrace reef zone, one on top of the buttresses, and one on the sides of buttresses. These belt-quadrats were made perpendicular to shore because of an observed gradient in coral composition along the length of the top of each buttress, and because the buttress tops were quite narrow. Species-area curves began to level out in 15-20 frames (Fig. 3), requiring the combination of the two belt-quadrats at each depth. Vertical extensions of colonies and hidden sections of corals were not included in the measurements.

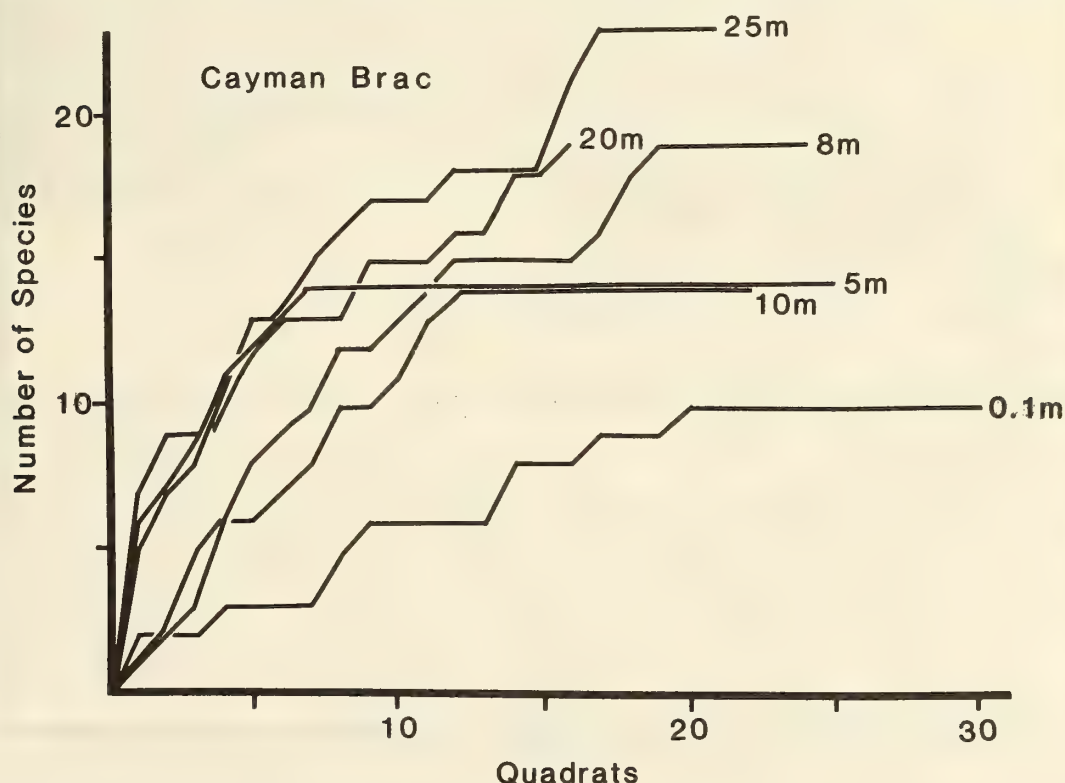


Figure 3. Species-area curves for Cayman Brac.

Zooxanthellate, constructional (Schuhmacher and Zibrowius, 1985) coral species were identified in the field by the author, using Almy and Carrion-Torres (1963), Roos (1971), Smith (1971), Wells (1973), and Humann (1983), in addition to the references given in Fenner (1988).

The taxonomic system of Wells and Lang (1973) as modified by Cairns (1982) was used, since several of the species synonymized by Zlatarsky and Estallela (1982) are separable on biological criteria (e.g., Lang, 1971; van Moorsel, 1983; de Weerd, 1984; Szmant, 1986; Fenner, in press). *Agaricia humilis* was not distinguished from *Agaricia agaricites* in transects due to time limitations, nor was *Agaricia lamarcki* distinguished from *Agaricia grahamae*. Azooxanthellate, non-constructional species were

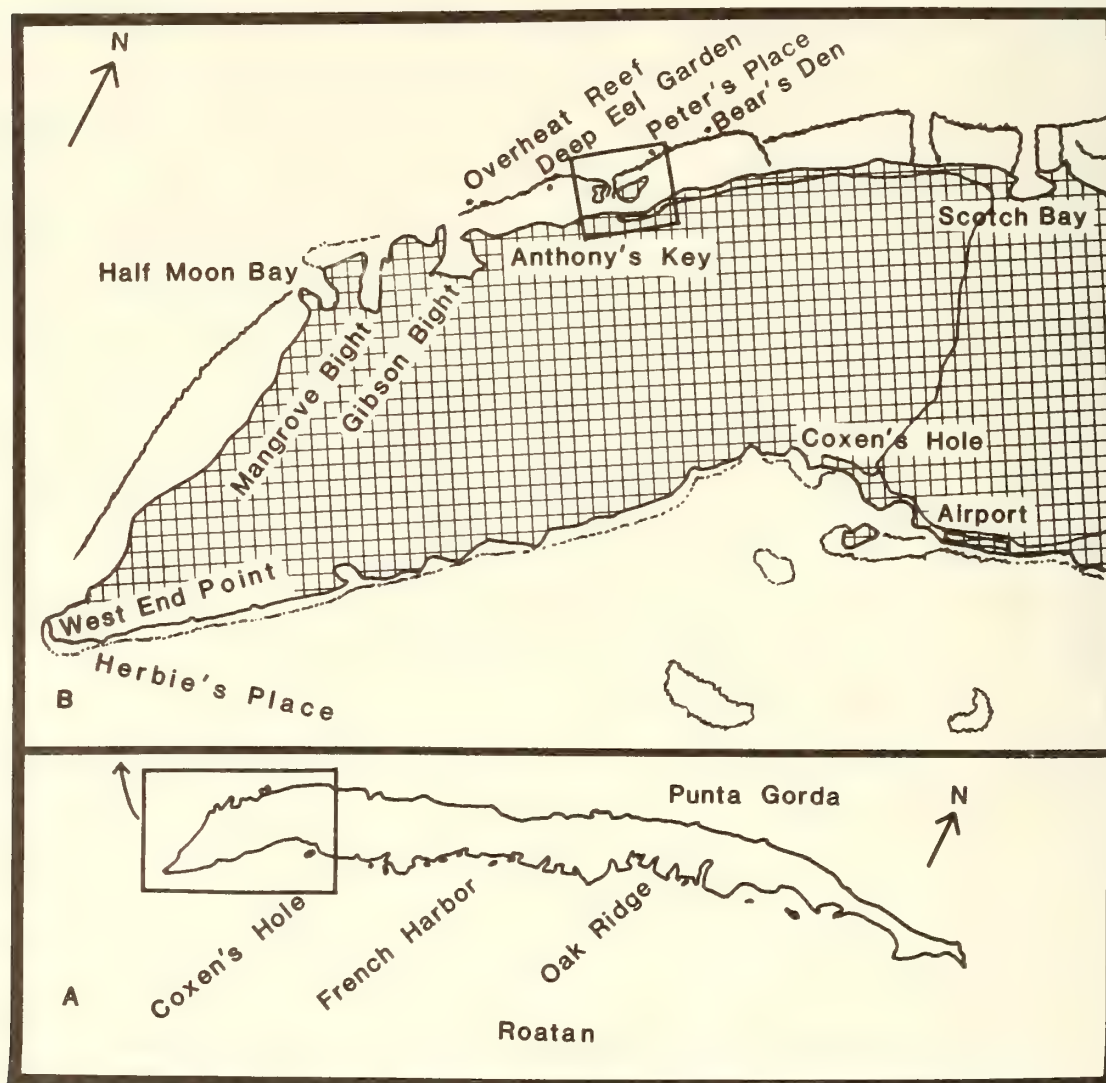


Figure 4. Maps of Roatan study area. A. Roatan. B. Western Roatan. A redrawn from Wilensky, 1974. B redrawn from Davidson, 1974.

identified by S. Cairns from specimens deposited at the U.S. National Museum, except for *Thalamophyllia riisei*, a distinctive species which was identified in the field by the author. Shannon and Weaver's diversity index H'_C was calculated using coverage measures ($H'_C = p(\ln p)$), as was the evenness index ($J = H'_C / H'_C \text{max}$) (Pielou, 1969).

RESULTS

Roatan

The coast of northwestern Roatan is bordered by a fringing reef (Fig. 4). Six zones were distinguished: lagoon, crest, shallow forereef, spur-and-groove, deep forereef, and deep forereef slope.

Lagoon

The lagoon was visually surveyed east of Anthony's Key, and west of Bailey's Key (Fig. 4B & 5) at about $86^{\circ}35'W$, $16^{\circ}20'N$. On the east side of Anthony's Key, the lagoon is about 365 m wide. It is about 1 m deep behind the reef

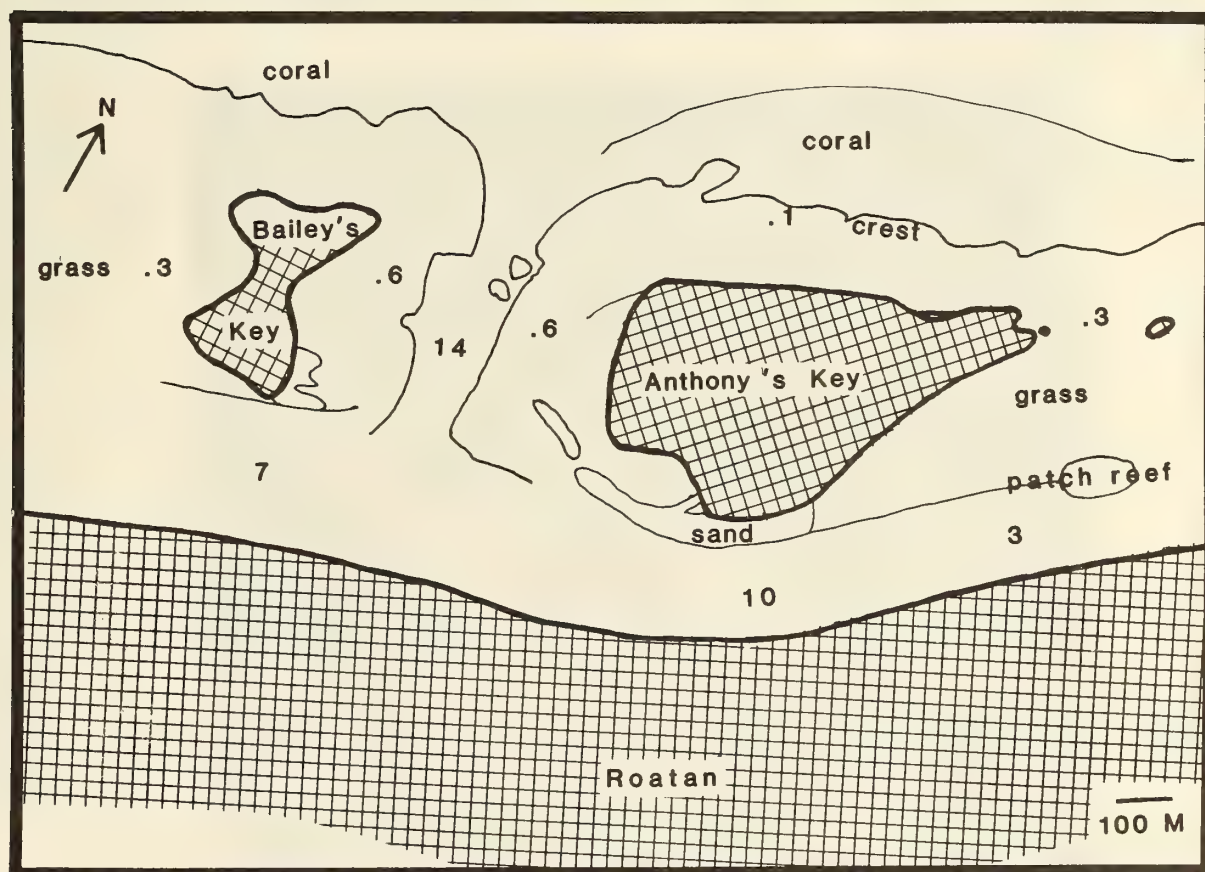


Figure 5. Anthony's Key area, northwest Roatan. Redrawn from areal photograph in Wilensky (1979). Depths in meters.

crest, deepening to about 3 m within about 100 m of the shore of Roatan. Coral heads and clumps of *Porites porites* forma *furcata* were found in the outer part of the lagoon. The middle and inner parts of the lagoon have an almost continuous bed of the seagrass *Thalassia testudinum*, with a dense community of the anemone *Bartholomea annulata*. Bare sand spots are burrowed by the heart urchin *Meoma ventricosa*.

Crest

The reef crest rises vertically from the lagoon to a depth of about 10 cm. During low tide, the reef top is emergent, and waves break over the crest. The crest is about 3 or 4 meters wide, and its upper surface consists of coral rock covered with brown algae (e.g., *Sargassum* and *Turbinaria* sp.) and crustose (e.g., *Porolithon pachydermum*) and articulated (e.g., *Amphiroa* sp.) coralline algae (Fig. 6). The vertical surface on the lagoon side supports living corals, primarily *Agaricia tenuifolia*. The line transect revealed that only 7.5% of the surface is covered with living corals, with *A. tenuifolia* covering 4.8%, *Porites astreoides* covering 1.3%, and five other species covering smaller areas.



Figure 6. Reef crest, 0.1 m depth, Anthony's Key, Roatan. Left center, *A. tenuifolia*.

Shallow forereef

The reef front can be divided into four zones. The shallowest zone is the shallow forereef which has corals

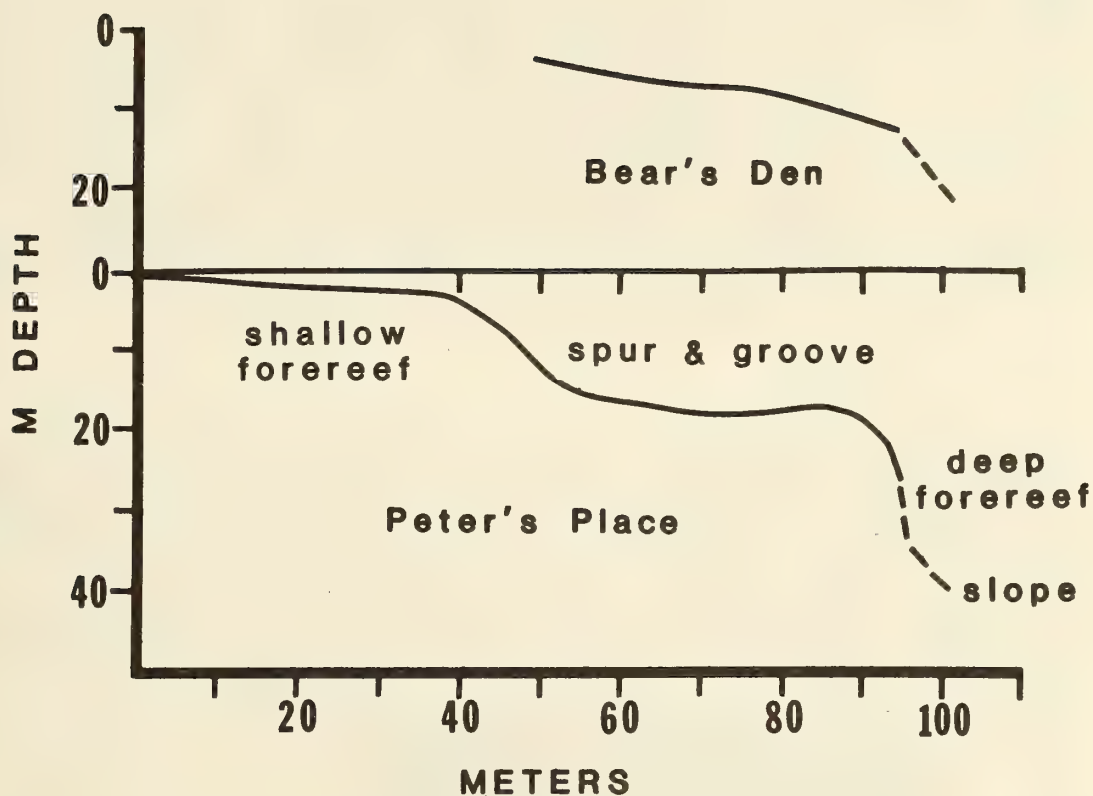


Figure 7. Depth profiles of two Roatan reefs, each taken from one transect. Dotted line extensions observed but not measured.



Figure 8. Shallow Forereef, 3 m deep, "Overheat Reef", Roatan. Right, *M. annularis*.

scattered on a relatively flat coral rock base, extending to about 5 m depth (Fig. 7 & 8). The coral rock is nearly completely covered with crustose coralline algae and bears many chiton holes about 1 cm in diameter (Littler et al., 1989, p.220-221). The sea urchin *Diadema antillarum* is uncommon, yet green and brown algae are also uncommon, probably due to common herbivorous fish. Photo belt-quadrats revealed that 18% of the surface is covered with corals. The hydrocoral *Millepora complanata* covers 5.7%, *Diploria strigosa* 4.2%, *A. tenuifolia* 2.9%, *Siderastrea siderea* 2.2%, *Montastrea annularis* 1.4%, *Diploria clivosa* 1.1%, and six other corals cover smaller areas.

Spur-and-groove

The shallow forereef grades into a spur-and-groove zone dominated by massive *M. annularis* colonies on the tops of the buttresses, and dissected by grooves or sand channels. At some locations a dropoff separates these two zones, as it does at "Peter's Place" buoy, while at other locations such as "Bear's Den" buoy (both at about 86°34'W, 16°20'N), no such sharp demarcation exists (Fig. 7). The grooves or sand channels are often only 1-2 m wide, and run parallel to each other down the forereef slope (perpendicular to the shore). In places, some of the sand channels widen considerably, to a width of 12 m or more, known locally as 'white holes'. The grooves vary in depth, but in places extend to about 5 m below the adjacent reef tops. Their sides support less living coral than the spur tops, and their bottom is



Figure 9. Spur top, 8 m depth, "Gibson Bight", Roatan. All visible coral is *M. annularis*.

typically flat and covered with rounded loose coral rubble up to 30 cm in diameter, resting on sand. In some locations, living *M. annularis* grows in flattened colonies out over the groove, closing a ceiling over a small tunnel, most often at the deeper end of this zone. The coral buttresses growing between the grooves are often 3-5 m wide (Fig. 9). The quadrat photos were taken only on the tops of buttresses. The two photo belt-quadrats revealed that 28.8% of the surface is covered with corals. *M. annularis* covers 22.7%, *A. tenuifolia* covers 4.1%, and nine other species cover smaller areas.

Deep forereef

At a depth of about 12 to 18 m, a sharp increase in slope marks the beginning of the deep forereef. In most locations, e.g. "Peter's Place" (Fig. 7), the deep forereef descends at an angle just less than vertical. Many corals grow on the surface in flattened colonies projecting from the slope as shelves (Fig. 10). Spaces between corals are dominated by brown algae (e.g., *Lobophora variegata*, *Dictyota* sp.). Although *M. annularis* is clearly present, it

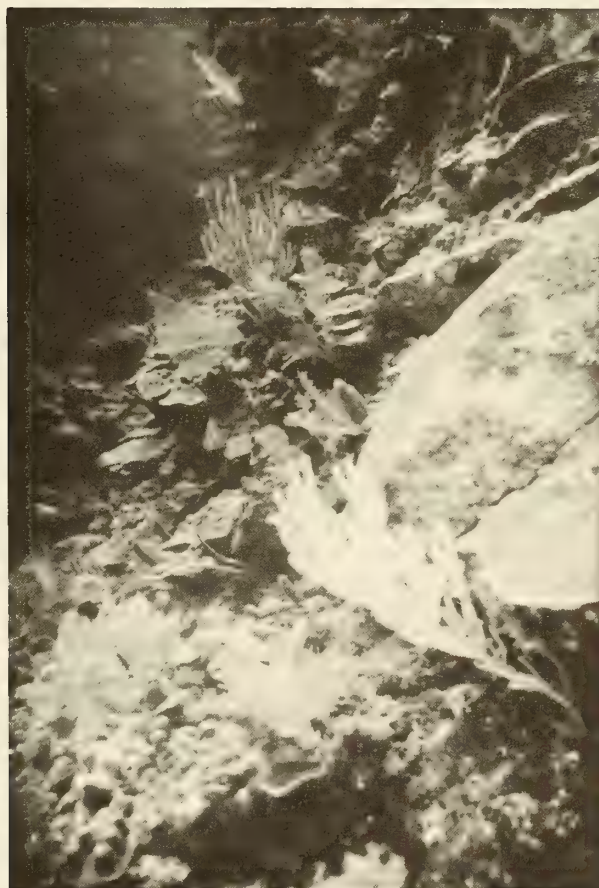


Figure 10.
Deep Forereef,
15 m depth,
"Gibson Bight".
Center right:
C. natans and
M. annularis.

does not appear as prevalent as in the spur-and-groove zone. The undersides of projecting corals are dominated by pink crustose coralline algae, with few sponges or ahermatypic corals. Such coral overhangs rarely extend more than 1 m. Thus, they correspond closely to the overhangs and mouths of caves at Grand Cayman (Logan, 1981). The deeper grooves found in the forereef zone extend over the edge onto the deep forereef in a modified form. On the deep forereef they typically are less than 1 meter deep, and their floor and sides are covered with living coral. The two photo belt-quadrats showed that 28% of the surface is covered with coral. *M. annularis* covers 16.5%, *Colpophyllia natans* 3.4%, *P. astreoides* 1.8%, *D. strigosa* 1.6%, *Montastrea cavernosa* 1.5%, *A. agaricites* 1.4%, *A. tenuifolia* 1%, and nine other species cover smaller areas. Averaged over the 4 zones, *M. annularis* is the most common coral at Roatan, covering 10.3%, followed by *A. tenuifolia* with 3.2%, *M. complanata* 1.6%, and *D. strigosa* 1.4%.

Deep forereef slope

Although the deep forereef slope was not reached in this study, the bottom could be seen to assume a slope of about 45° at a depth of about 35 m. This deep slope appeared to have fewer corals, separated by a sandy bottom.

South shore

Observations were also made at three locations on the southwestern shore of Roatan. "Mary's Place", near French Harbor (Fig. 4A), has a 2 m-wide cleft in the reef that parallels the reef front and extends from the reef surface at a depth of about 12 m to below 35 m. In the cleft the undersides of projecting corals have azooxanthellate, non-constructural coral communities (e.g., *Colangia immersa* and *Paracyathus pulchellus*) in addition to crustose pink coralline algae. The reef at Dixon Cove, between French Harbor and Coxen's Hole (Fig. 4A), has an almost pure stand of *Acropora cervicornis* offshore at a depth of about 5 m. The steep forereef from about 12-15 m on down appears very similar to the same zone on the northwest shore of Roatan, and below it a deep forereef slope appears similar to the same zone on the northwest shore. At "Herbie's Place", near West End Point (Fig. 4B), the reef slopes continuously from the shoreline outward, at an angle of about 45°. Coral cover is less than on the forereef of northwest Roatan, but there are more sponges and gorgonians. No signs of coral bleaching or disease were seen at any location in Roatan.

Diversity

A total of 40 species and 2 forms of Scleractinia were found in Roatan, plus 3 species of hydrocorals, as listed in

	Roatan	Cayman Brac	Little Cayman
<i>Manicina areolata</i> forma <i>areolata</i>	4		
forma <i>mayori</i>			5
<i>Colpophyllia natans</i> (=breviserialis)	2	2	3
<i>Montastrea annularis</i>	1	1	1
<i>Montastrea cavernosa</i>	3	2	2
<i>Colangia immersa</i> +	5*		5*
<i>Caryophyllia</i> sp. +			5*
<i>Meandrina meandrites</i> forma <i>meandrites</i>	4	4	4
<i>Dichocoenia stokesi</i> (=stellaris)	4*	4	4
<i>Dendrogyra cylindrus</i>	3	5	
<i>Mussa angulosa</i>	5	4	5
<i>Scolymia cubensis</i>	5	4	4
<i>Isophyllia sinuosa</i>	4*	5*	5*
<i>Isophyllastrea rigida</i>	4	4*	5*
<i>Mycetophyllia lamarckiana</i>	4	3	4
<i>Mycetophyllia danaana</i>	4	3*	4*
<i>Mycetophyllia aliciae</i>	4	5*	3*
<i>Mycetophyllia ferox</i>	4	4	4
<i>Mycetophyllia reesi</i>			4*
<i>Thalamophyllia riisei</i> (?) +	5*		
<i>Eusmilia fastigiata</i> forma <i>fastigiata</i>	4	4	4
<i>Balanophyllia grandis</i> (?) +	5*	4**	5**
<i>Paracyathus pulchellus</i> (=defilippi) +	5*		
<i>Paracyathus</i> sp.	5*	5**	
<i>Millepora alcicornis</i> #	3	4*	3*
<i>Millepora complanata</i> #	2	3	3
<i>Stylaster roseus</i> #+	4*	4	4

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1 = common          2-4 = intermediate          5 = rare
+ azooxanthellate non-constructive (ahermatypic)
* new report for this island          # hydrocoral
** new report for the Cayman Islands
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Coral cover was greatest on the spur-and-groove zone (spur tops) and steep forereef slope, but coral diversity was greatest on the shallow forereef and deep forereef. Measures of coral cover and diversity are presented in Table 2. The number of species was least at the crest, and greatest at the deep forereef. Coral cover was lowest at the crest, and highest on the spur-and-groove zone (spur tops) and deep forereef. The diversity index H'_C was greatest in the shallow forereef, intermediate at the deep forereef, and lowest at the spur-and-groove zone and crest. The evenness index J showed a pattern similar to H'_C , except that the crest had an intermediate value. Together these indices reveal a pattern of increasingly dense coral populations with depth to at least 8 m depth. Species diversity was lowest in the shallowest zone and in an intermediate depth zone (spur-and-groove zone, spur tops) where one species (*M. annularis*) was dominant. Below about

35 m the coral populations appear less dense.

Table 2

Coral diversity at Roatan. Number of quadrats at "Overheat Reef", OR; Number of quadrats at "Deep Eel Garden", DEG; Number of species, S; percent living coral coverage, % Cov.; Shannon and Weaver's diversity index, H'_C ; species evenness, $J' = H'_C / H'_{Cmax}$.

Zone	Depth	OR	DEG	S	% Cov.	H'_C	J'
crest	.1m			8	7.5%	1.18	.57
shallow forereef	3m	10	19	12	18.2%	1.96	.76
spur and groove	8m	10	23	11	28.8%	.82	.34
deep forereef	15m	9	23	15	28.3%	1.54	.57

Cayman Brac

Depth profile

Coral reefs surround most of Cayman Brac (Logan, 1988; in press), including the southwestern area studied (Fig. 11). Unlike most of the reef surrounding Cayman Brac, the study reef breaks the surface offshore, and is separated from the shore by a shallow lagoon. Six zones associated with the reef are distinguished here, based on the nomenclature of Logan (in press), Roberts (e.g., 1977; in press), and Rigby and Roberts (1976): lagoon, crest, shallow terrace, terrace reefs, deep terrace, and deep forereef. The lagoon's depth profile was measured at Channel Bay, (Fig. 11B) at about 79°53'W, 19°41'N.

The lagoon at Channel Bay is about 125 m wide (Fig. 12), and no more than 1 m deep. The lagoon in the study area, like the other zones, appears as described in Logan (in press), except as noted below. Several small patch reefs near the seaward margin of the lagoon are about 2-3 m in diameter, with steep sides and a flat top. They rise from the bottom in about 1 m of water to within about 20 cm of the surface. The reef crest rises gradually from the lagoon to a depth of about 10 cm. The crest is about 50 m wide. Most of the width of the crest dips slightly away from land, reaching about 30 cm depth at the seaward margin. A depth profile of the shallow terrace and the terrace reef was taken at "Heddie's Reef" buoy at about 79°51'W, 19°41'N) from a depth of 3 m to a depth of 15 m (Fig. 12). Although the depth profile taken did not extend through the surf to

the crest, extrapolation indicates the width of the omitted area to be about 120 m. The shallow terrace ends abruptly in spurs (Fig. 12). The spurs or buttresses are quite narrow, only 1-2 m wide at their top. They extend in nearly straight lines perpendicular to the shore, and their crests describe an irregular profile (Fig. 12). The grooves or

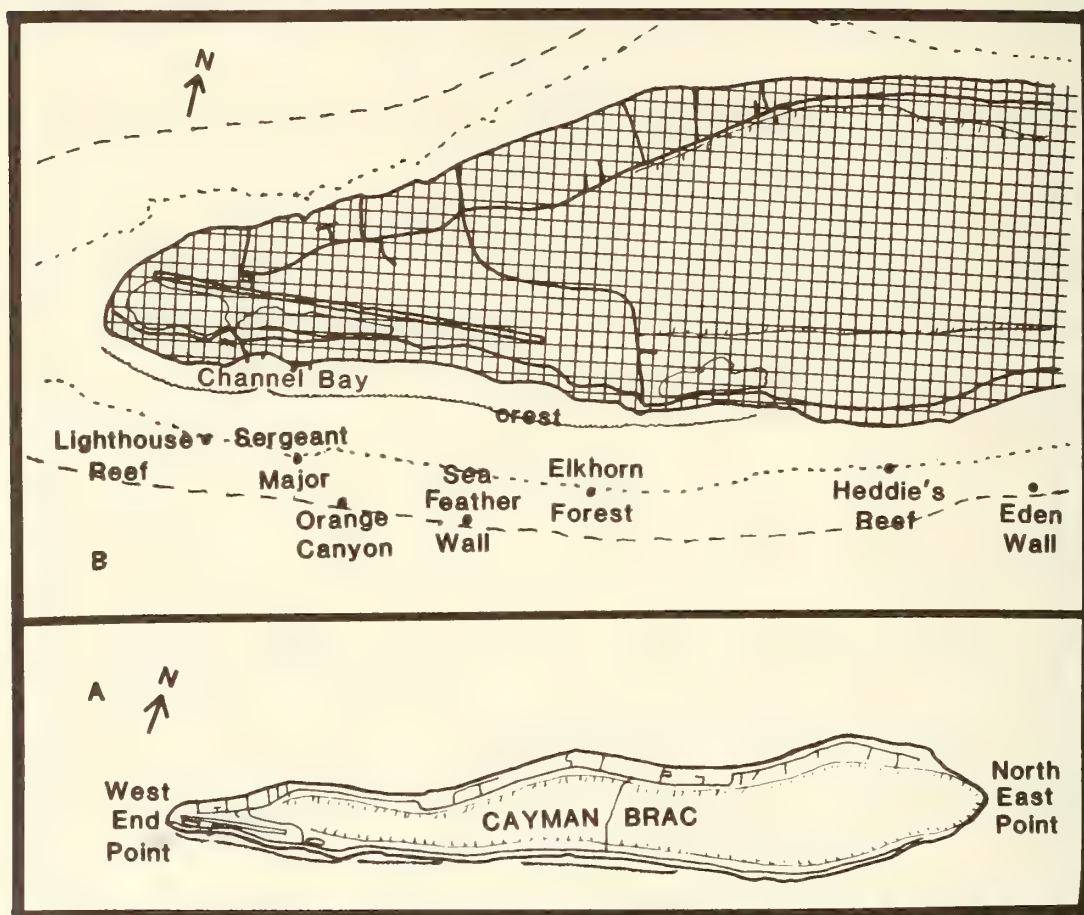


Figure 11. Maps of Cayman Brac study area. A. Cayman Brac. B. Western Cayman Brac. A redrawn from British Admiralty chart #462 of the Lesser Caymans. B redrawn from Logan (1988).

sand channels between the spurs are about 2-5 m wide. The spurs in the terrace reef end abruptly by falling sharply to meet the sand channel bottom and the deep terrace at a depth of about 15 m (Fig. 12). A depth profile of the deep terrace and deep forereef was taken at "Eden Wall" buoy ($79^{\circ}51'W$, $19^{\circ}41'N$). The entire width of the deep terrace was not measured due to time limitations; however, it is estimated to be 100-200 m wide. At a depth of about 18 m, the bottom dips at a steep angle, marking the boundary between the deep terrace and deep forereef, and reaching nearly vertical by a depth of 25 m (Fig. 12). At some

locations, such as "Eden Wall", where the depth profile was taken, the deep forereef continues to descend vertically to what appears to be about 50 m, and then descends at about 45° . In other locations, a 45° slope cannot be seen from 30 m depth, while elsewhere the deep forereef descends at less than vertical, though always at a steeper angle than 45° .

Coral populations

In the lagoon, areas of coral rubble bottom have a sparse community of small corals, mainly *Siderastrea radians*. A belt-quadrat of rubble bottom revealed only 2% of the bottom is covered with live coral, and the diversity is quite low ($H'_C = .87$, Table 3). *S. radians* covers 1% of the bottom, and only 4 other corals were found in the transects. Coral cover appears greater on the sides of patch reefs than their tops. A belt-quadrat composed of grid placements on top of the patches revealed 6 species of corals, covering 22% of the surface with an intermediate diversity ($H'_C = 1.45$, Table 3). Four species of coral are most common on the patch reefs: *P. porites* f. *furcata* (7.8%), *A. agaricites* (5.8%), *M. annularis* (4.3%) and *P. astreoides* (3.6%).

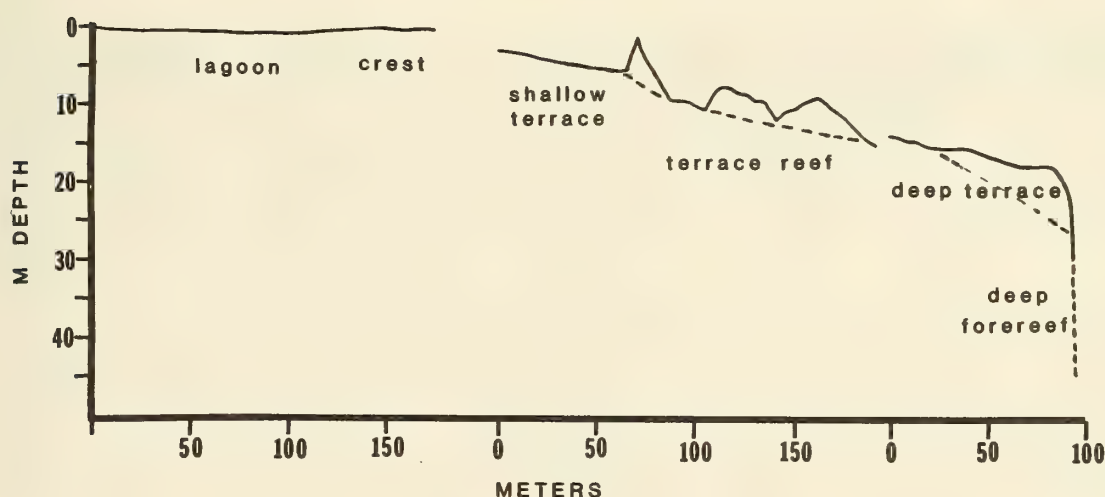


Figure 12. Depth profiles of southwest Cayman Brac reefs. The lagoon and crest were measured in Channel Bay, in front of the Brac Reef Hotel, the shallow terrace and terrace reef were measured at "Heddie's Reef", and the deep terrace and deep forereef were measured at "Eden Wall".

A belt-quadrat on the reef crest revealed 10 species of coral covering just 2% of the bottom, with an intermediate diversity ($H'_C = 1.58$, Table 3). *P. porites* f. *furcata* is the most common coral in this zone, with 1.1% cover. A

belt-quadrat on the shallow terrace revealed 14 species of coral covering 12% of the bottom with the highest diversity found on the reef ($H'_C = 1.96$, Table 3). The most common corals on the shallow terrace are *D. strigosa* (3.2%), *P. astreoides* (2.3%), *S. siderea* (2.1%), and *M. annularis* (1.6%).

The crests of spurs of the terrace reef are dominated by massive *M. annularis* (Logan, in press) at their seaward end, and have scattered large *Acropora palmata* colonies on their middle and shoreward crests. The sides of the spurs have *M. annularis* extending down over their seaward end. A belt-quadrat on the top contained 19 species of corals, covering 30% of the surface with a moderate diversity ($H'_C = 1.65$, Table 3). *A. palmata* (11.1%) is the most common coral, followed by *M. annularis* (7.5%), *M. complanata* (3.3%), *P. porites* f. *furcata* (2.3%), *C. natans* (1.7%), and platy *Agaricia* sp. (1.2%). Belt-quadrats taken on the sides of the spurs reveal 14 species of coral, covering 14% of the sides, with an intermediate diversity ($H'_C = 1.61$, Table 3). The most common corals are *M. annularis* (5.8%), platy

Table 3

Coral diversity at Cayman Brac. Number of species, S; percent of living coverage, % Cov.; Shannon and Weaver's diversity index, H'_C ; species evenness, $J' = H'_C/H'_{Cmax}$.

Zone	Depth	Sites*	S	% Cov.	H'_C	J
lagoon rubble	.5m	CB:11	5	1.6%	.87	.54
patch	.2m	CB:10	6	22.3%	1.45	.81
crest	.1m	CB:30	10	2.4%	1.58	.69
shallow terrace	5m	SM:25	14	11.6%	1.96	.74
buttress top	8m	EF:14,L:10	19	29.7%	1.65	.56
sides	10m	EF:14,L:10	14	13.6%	1.61	.61
deep terrace	20m	OC:11,SF:5	19	44.6%	1.94	.66
deep forereef	25m	OC:10,SF:11	23	33.8%	1.87	.60

*CB = Channel Bay, in front of Brac Reef Hotel (79°53'W, 19°41'N). SM = "Sergeant Major Reef" (79°53'W, 19°41'N). EF = "Elkhorn Forest" (79°52'W, 19°41'N). L = "Lighthouse Reef" (79°53'W, 19°41'N). OC = "Orange Canyon" (79°53'W, 19°41'N). SF = "Sea Feather Wall" (79°53'W, 19°41'N). Number is number of quadrats at that location.

Agaricia sp. (4.0%), and *P. astreoides* (2.3%). Belt-quadrats were also taken on the reef near the seaward end of the deep terrace. Nineteen species of coral were found in these belt-quadrats, covering 44% of the bottom, with a high level of diversity ($H'_c = 1.94$, Table 3). *M. annularis* is the most common species of coral (16.6%), followed by *M. cavernosa* (7.5%), *C. natans* (6.4%), *P. porites* f. *furcata* (4.1%), *A. agaricites* (3.0%), *Stephanocoenia michelinii* (2.3%), *D. strigosa* (1.9%), and *P. astreoides* (1.0%).

Belt-quadrats were taken on the deep forereef at a depth of about 25 m. Twenty-three species of coral were found in the belt-quadrats, covering 33% of the surface with a high diversity ($H'_c = 1.87$, Table 3). *M. annularis* is most common (Logan, in press) in this zone (16.2%), followed by *M. cavernosa* (5.2%), *C. natans* (3.1%), platy *Agaricia* sp. (1.8%), *P. astreoides* (1.5%), *A. agaricites* (1.3%), and *S. michelinii* (1.0%). When averaged across all zones, *M. annularis* was the most common coral, with 6.5% cover, followed by *P. porites* f. *furcata* with 2%, *M. cavernosa* (1.8%), *A. agaricites* (1.4%), *P. astreoides* (1.4%), *C. natans* (1.4%), and *A. palmata* (1.4%). Total coral cover averaged 20%.

Diversity

A total of 40 species and 3 forms of Scleractinia were found on Cayman Brac, plus 3 species of hydrocorals, as listed in Table 1. Five of the Scleractinia are azooxanthellate and non-constructive. Corals found both in and out of the belt-quadrats were included in this count. Twenty-four species of stony corals are new records for Cayman Brac, as indicated in Table 1.

The richest coral communities are on the deep terrace and deep forereef. The poorest coral communities are on lagoon rubble and on the reef crest. Measures of coral cover and diversity are presented in Table 3. The number of species in transects increases with depth throughout the range studied, except that spur tops have more species than their sides. The percentage of surface covered by coral increases up to the end of the deep terrace, at about 18 m depth, except for spur tops which have higher coverage than their sides, and a high coverage on lagoon patch reefs. The diversity index H' also increases with depth to the deep terrace, except for higher values on the spur tops than on their sides, and a high value on the shallow terrace. The evenness index J showed no overall trend. Together these indices reveal a pattern of increasingly dense and diverse coral populations with depth to at least 18 m depth. Spur tops consistently have greater coral coverage and diversity than the spur sides (which are deeper) perhaps as an edge effect due to reduced sedimentation (Porter, 1972). Below

about 35 m, the coral populations appear less dense.

Little Cayman

Little Cayman is surrounded by fringing reef, enclosing a shallow lagoon (Logan 1988; in press). Zonation of this reef is similar to that on Cayman Brac and Grand Cayman, except for a short section of the study site at Bloody Bay, on the northwestern shore at about $80^{\circ}5'W$ $19^{\circ}41'N$. In this area, the reef does not reach the surface offshore, and there is no lagoon. Thus, four zones can be distinguished: shallow terrace, terrace reef, deep terrace, and deep forereef. In the center section of Bloody Bay, the shallow terrace extends to the edge of the deep forereef, omitting the terrace reef and deep terrace (Logan, in press; Fig. 13).

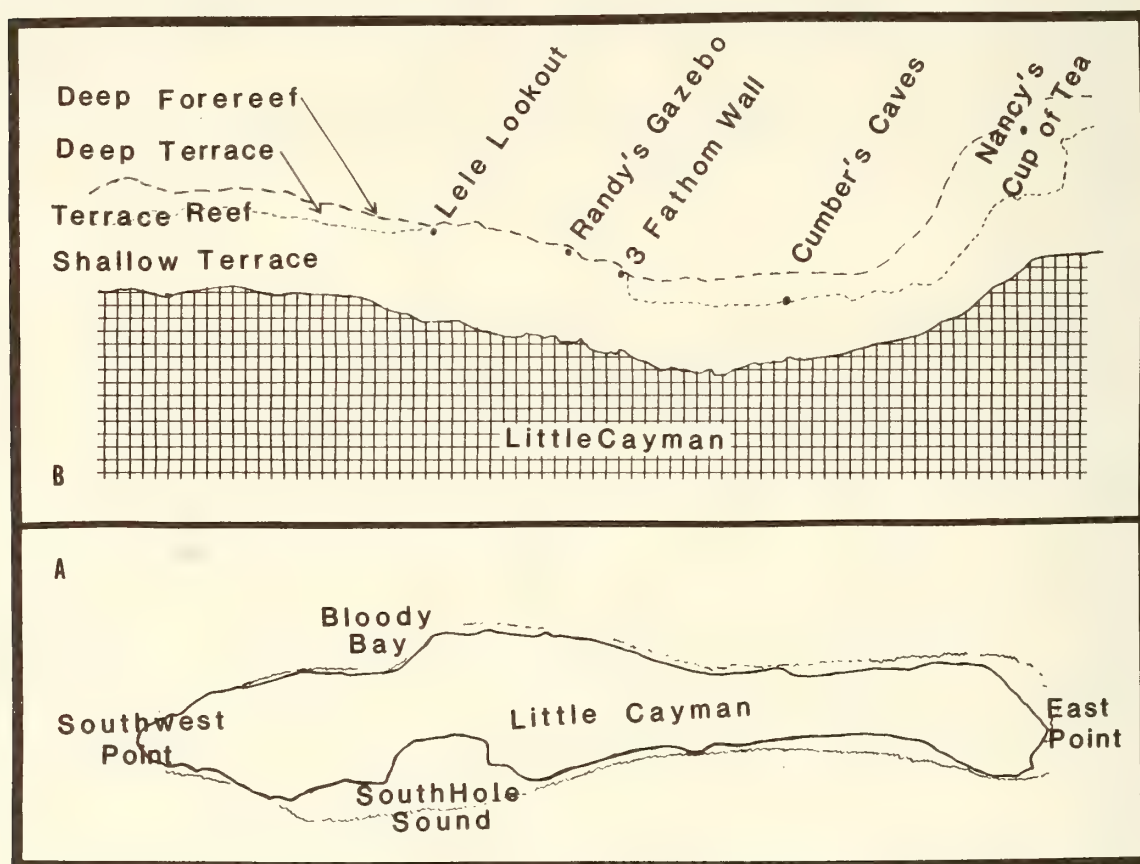


Figure 13. Maps of Little Cayman study area. A. Little Cayman. B. Bloody Bay. A redrawn from British Admiralty chart #462 of the Lesser Caymans. B redrawn from Logan (1988) and Cayman Aggressor captain's sketch.

A depth profile of the reef where there are four zones was taken at "Cumber's Caves" buoy at $80^{\circ}5'W$ $19^{\circ}41'N$, and shown by the lower trace in Fig. 14. A gently dipping

terrace extends from the shoreline about 100 m out to a depth of about 6 m. The terrace reef extends up to 20 m horizontally from a depth of about 6-13 m. Only one groove was found in the terrace reef, at "Cumber's Caves" (Fig. 13), and it extends only a short way into the base of the escarpment.

The deep terrace consists of a gently sloping plane of sand, about 65 m wide, and from 13 to 17 m deep. In areas such as "Nancy's Cup of Tea" buoy (Fig. 13) buttresses of coral extend to connect the terrace reef with the deep forereef (Logan, in press). Buttresses appear to be about 10-30 m wide, and the intervening sand 100-200 m wide. At the outer edge of the deep terrace, coral grows upward abruptly, with overhangs present at some locations. A crest is reached at about 13 m depth. Then the reef dips downward at an angle that increases to near vertical by 25 m depth, and continues at that angle to at least 35 m depth.

In the central section of Bloody Bay, only two zones remain: shallow terrace and deep forereef (Logan, in press).

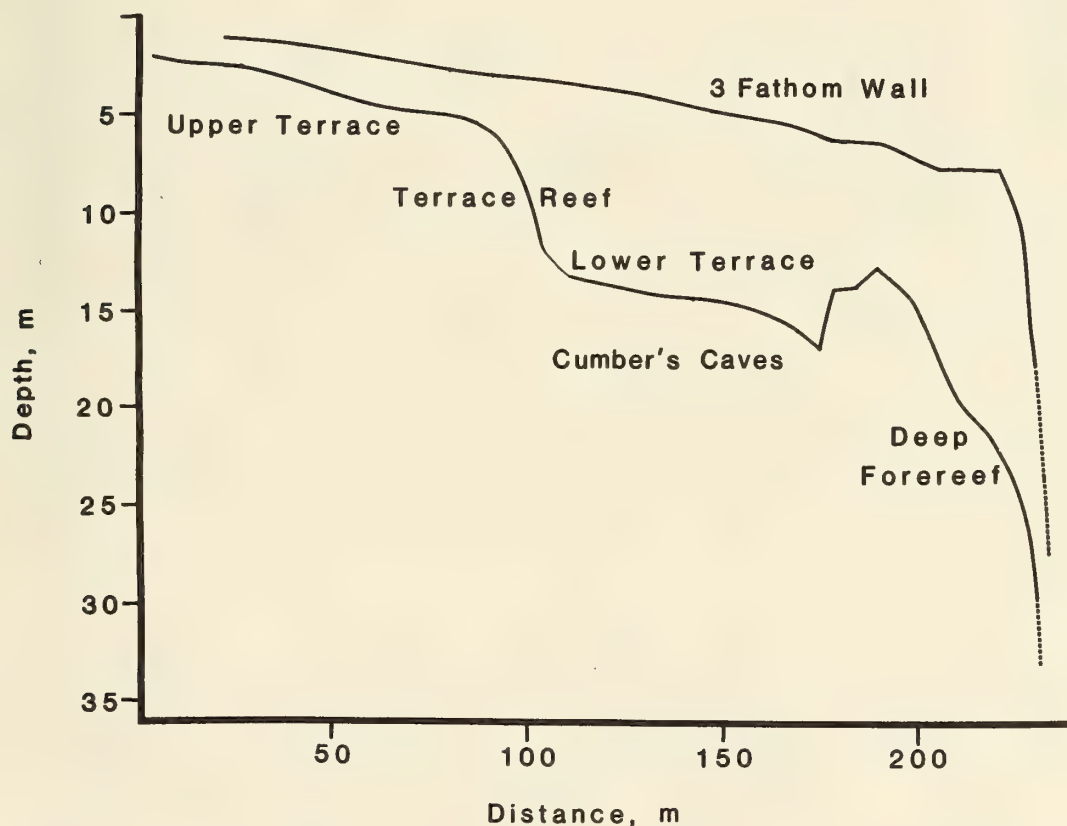


Figure 14. Depth profiles of Bloody Bay, northwest Little Cayman. The upper curve was measured at "3 Fathom Wall", and the lower curve at "Cumber's Caves". The curves are not offset.

This is formed by the terrace reef escarpment curving out to join the deep forereef at each end of this section (Fig. 13). In this central section, the shallow terrace extends from the shoreline out about 250 m to a depth of about 6-8 m, where the bottom dips steeply as the deep forereef. This can be seen in a depth profile (Fig. 14, top trace) taken at "3 Fathom Wall" buoy ($80^{\circ}5'W$, $19^{\circ}41'N$). The deep forereef in this area is a very steep, smooth wall that has a covering of scattered corals and sponges.

Diversity

Thirty-nine species and 3 forms of scleractinia and 3 species of hydrocorals were found at Little Cayman (Table 1). Twenty species of stony corals were reported for the first time for Little Cayman, as indicated in Table 1.

DISCUSSION

The reefs of northwestern Roatan, Little Cayman, and southwestern Cayman Brac all feature a 15-20 m deep terrace above a steep forereef wall. Deep terraces are common in coral reefs around the world, and have been called the "Ten-Fathom Terrace" (Stoddart, 1969). All three of the Cayman Islands are surrounded by such a terrace (Rigby and Roberts, 1976; Roberts, 1977; in press; Logan, in press). However, one short section of Bloody Bay, on northwest Little Cayman, lacks a deep terrace for unknown reasons (Logan, in press; Fig. 13). The southern shore of Roatan has a terrace at 10-12 m depth that may correspond to the "Ten-Fathom Terrace", or to a shallow terrace common on many Caribbean reefs. The shallow terrace in the Cayman Islands is typically 6-10 m deep at its deep end (Rigby and Roberts, 1976; Logan, in press; Fig. 12, 14). Such a terrace, here called the "shallow forereef" was found at one location on northwest Roatan, but not at a second location, for unknown reasons. Some other Western Caribbean reefs show similar terrace features (Belize: Rutzler and Macintyre, 1982b; Chinchorro: Jordan and Martin, 1987; Cozumel: Fenner, 1988), though others may not (Yucatan: Jordan, 1979).

The reef off the northwest coast of Roatan has a very regular and well-developed spur and groove, or buttress and sand channel system. The grooves are common, oriented at right angles to the crest, and fairly uniform in dimensions. It is unusual for a spur and groove system to be found along a leeward shore (Stoddart, 1969), though they do exist along some leeward shores (e.g., Puerto Rico: Morelock et al., 1977; Barbados: Stearn et al., 1977; Grand Cayman: Logan, 1981; Cozumel: Fenner, 1988). In some cases where a spur and groove system exists on the leeward side of an island, the spurs and grooves are smaller and less well organized than on the windward side (Roberts, 1974; Jordan and Martin,

1987). And yet northwest Roatan, western Barbados, and southwest Puerto Rico have well organized spur and groove systems. The slope of a reef is an important factor in addition to the amount of wave action in producing an ordered spur and groove system. As Woodley and Robinson (1977) point out, good sediment drainage allows the growth of spurs. Sloping reef fronts, like wave action, promote sediment drainage, allowing spur and groove formation.

The coral populations at Roatan and Cayman Brac are not unusual for the Western Caribbean. A total of 44 taxa of stony corals were found at Roatan, compared to 47 found there by Halas and Jaap (1982) (according to the taxonomic system of Wells and Lang (1973) as modified by Cairns (1982)). Nine taxa reported here were new reports for Roatan, bringing the total reported at Roatan to 56. A total of 47 taxa were found on Cayman Brac and 45 on Little Cayman, compared to 25 for both these islands by Logan (in press), and 56 for Grand Cayman by Roberts (in press), Logan (1981), and Fenner (unpublished report of *Thalamophyllia riisei*). Twenty-four taxa were new reports for Cayman Brac, and 20 for Little Cayman, but only four were new for the Cayman Islands as a whole. The number of coral taxa reported here are similar to those reported from other western Caribbean reefs at Belize: 53 (Cairns, 1982) and Chinchorro Banks, Mexico: 47 (Jordan and Martin, 1987), but less than that at (more intensely studied) Cozumel: 71 (Fenner, 1988; Jordan, 1988; Muckelbauer, 1990; Fenner, in press; Fenner, unpublished report of *Madracis formosa*, *Manicina areolata* f. *mayori*, *Porites colonensis* (Zlatarski, 1990), *Eusmilia fastigiata* f. *flabelliformis*, *Oculina* sp., *Montastraea annularis* sp. 2 & 3 (Knowlton, et al., 1992), and *Madrepora carolina*). There are a wide range of numbers of coral taxa reported from regional reefs, from 16 at Swan Islands (Tortora and Keith, 1980) and 36 at Yucatan reefs (Jordan et al., 1981) to 78 in Jamaica (Wells and Lang, 1973; Cairns, 1986; Fenner, 1988; Knowlton, et al., 1992, Fenner, in press). The differences appear to be primarily a function of the extent of study of a location (Liddel and Ohlhorst, 1988); the total number of corals on many Caribbean reefs may be close to that found in Jamaica after intensive study.

Liddel and Ohlhorst (1988) suggested that the number of species found in transects would be a better indicator of diversity than total species lists. They compared the number of scleractinian species found in transects at about 15 m depth at 12 locations in the Caribbean. From 11 to 20 species were found in these transects, with a mean of 15 species. In the present study, 14 coral species were found at 15 m depth at Roatan (Table 2, *Millepora* removed), and 18 species were found at 20 m at Cayman Brac (Table 3, *Millepora* removed). In a previous study of Cozumel (Fenner,

1988), 18 species were found in transects at about 15 m depth (Table 2, *Millepora* and *Stylasterina* removed). Liddel and Ohlhorst (1988) reported that 14-28 scleractinia were found among all transects at the 12 locations, with an average of 20 species. In the present study, 21 scleractinia were found in Roatan transects, 31 at Cayman Brac, and in the previous study of Cozumel (Fenner, 1988) 28 were found. Thus, by these measures, coral diversity at Roatan was typical for a Caribbean reef, and Cayman Brac and Cozumel had relatively rich coral diversities.

Diversity indices derived from transect samples may not be as heavily biased in one direction by the total amount of effort expended as the total number of coral taxa reported. Shannon and Weaver's diversity index H'_c ranged from .82 to 1.96 in northwest Roatan, with an average of 1.38 over the four zones. The same index ranged from .87 to 1.96 in southwest Cayman Brac, with an average of 1.58 over the six zones. On Little Cayman, Logan (in press) reported an H'_c on the terrace reef of 1.63, which is very close to the values found in this study at Cayman Brac for terrace reef buttress tops (1.65) and buttress sides (1.61). The diversity of corals on other western Caribbean reefs have been reported at Panama, where H'_c was 1.95 (Porter, 1972), Yucatan where H'_c was 1.59 (Jordan et al., 1981), Cahuita (Costa Rica) 1.44 (Cortes and Risk, 1985), Jamaica 1.43 (Huston, 1985) and 1.35 (Liddel and Ohlhorst, 1987), and Cozumel 1.70 to 1.72 (Fenner, 1988; Muckelbauer, 1990). Liddel and Ohlhorst (1988) found that H'_c at about 15 m depth for 12 Caribbean locations averaged 2.0, with a range of 1.45-2.47. Roatan had an H'_c at 15 m of 1.54 (Table 2), Cayman Brac 1.94 (Table 3) and Cozumel 1.74 (Fenner, 1988, Table 2). Thus, this index indicates that Cayman Brac has a coral diversity similar to other western Caribbean reefs, and Roatan has slightly less coral diversity than other regional reefs.

Live coral cover on the Roatan and Cayman Brac reefs surveyed in this study was slightly low for the western Caribbean. Live coral cover ranged from 8 to 29% at Roatan, with the average being 21% cover. Coral cover ranged from 2 to 45% at Cayman Brac, averaging 20%. Logan (in press) reported 39% coral cover on the terrace reef of Little Cayman, which is more than that found in this study of Cayman Brac on the terrace reef buttress tops (29.7%) and buttress sides (13.6%). The average Cayman Brac cover of 20% and Roatan cover of 21% are more than the average 9% coral cover reported for the Yucatan (Jordan et al., 1981), but less than the 23% cover on the Belize Barrier Reef (Rutzler and Macintyre, 1982b), 28% to 32% cover at Cozumel (Fenner, 1988; Jordan, 1988; Muckelbauer, 1990; 15% after Hurricane Gilbert: Fenner, 1991), 37% to 41% cover at Jamaica (Huston, 1985; Liddel and Ohlhorst, 1987), 40% cover

at Cahuita, Costa Rica (Cortes and Risk, 1985), and 63% off southwest Grand Cayman (Cortes and Risk, 1985).

Thus, the number of coral taxa reported, the diversity index, and percent coral cover indicate that Roatan's northwestern reefs and Cayman Brac's southwestern reefs are well within the range reported for other western Caribbean reefs.

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CLASSIFICATION OF NON-MARINE ECOSYSTEMS

BY

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CLASSIFICATION OF NON-MARINE ECOSYSTEMS

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This review paper was originally prepared for the Classification Experts Meeting of the Project on Classification and Preliminary Inventory of Ecosystems in the South Pacific Region co-sponsored by the South Pacific Regional Environment Programme, The Nature Conservancy (TNC), and the East-West Center Environment and Policy Institute with funding provided by the United States Agency for International Development, the United States Fish and Wildlife Service, and the World Wildlife Fund - US (WWF - US) administered Biodiversity Support Project (TNC, WWF - US, World Resources Center). All of these agencies have a strong interest in finding and protecting the best representative examples of all native ecosystems in the tropical insular Pacific. This paper addresses some of the problems faced by those who would classify non-marine ecosystems in general and in the Pacific, and then gives particular attention to schemes (past and proposed) for non-marine ecosystem classification.

INTRODUCTION TO THE ECOSYSTEM CONCEPT

The concept of vegetation (versus flora) has seemed a fairly clear one for many years, as a term for the plant-cover of the earth, or any part of it (Egler 1942). Flora, often confused with vegetation, is used for any enumeration or account of the species that occur in a given area, region or other spatial unit.

Vegetation is an easy concept to grasp, as it is usually visible, and often characterized by apparently discontinuous variation, making it amenable to classification and mapping. There seems to be no suitable comparable term applying to animals or animal communities. Fauna is a comparable term to flora, an enumeration or account of the animal species in an area, region, or other spatial unit. Fauna is often also used for the zoological equivalent of the botanical concept of vegetation, but the use of the same term for two related concepts is not a satisfactory arrangement. However, a term for this equivalent zoological concept will not be coined here, as such a term should be very carefully chosen and agreed upon by at least a substantial number of zoologists and zoogeographers. Zoocoenosis would be a possibility, but the series of terms including this one, though very logical, has not met with general acceptance outside continental

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Europe. These terms will be discussed later in this paper along with other existing schemes.

von Bertalanffy is generally given credit for founding General Systems Theory (first codified in von Bertalanffy 1951). It was this theory, intended as a unifying concept for all scientific endeavor, along with the organismic theory of vegetation succession and climax (Clements 1928, 1936), that inspired Tansley to coin the term "ecosystem" in 1935 for a community of organisms interacting with their physical and biotic environment. There has always been a need for a more general term, inclusive of vegetation, its zoological equivalent, and the environment. Tansley's new term satisfied this need very well. He subsequently seldom used the term or concept, and it was not generally adopted for many years. Egler, in the 1940's or early 1950's, used it informally in correspondence. Francis Evans (1956), formally adopted and clearly defined it. It was then used, at least casually, by several American and Australian ecologists. In 1960, at the 10th Pacific Science Congress, Fosberg used and discussed the term "ecosystem" in a major symposium entitled "Man's Place in the Island Ecosystem" (Fosberg 1963). He also used it in a paper entitled "A Qualitative Description of the Coral Atoll Ecosystem" (Fosberg 1961b), which did not receive wide notice. In the introduction to the 1960 symposium, Fosberg discussed the concept in the sense that we will use it in the present paper. For a more complete history, see Major (1969).

Sukachev's Terminology: Over several decades, Professor V. N. Sukachev [W. N. Sukatschew] developed a system for classifying Russian ecosystems incorporating both organisms and environment (Sukachev 1945). His system of terminology, or parts of it, has appeared in various Central European works, but it has never been accepted by Anglo-American writers. His terms "biocoenosis," "phytocoenosis," "zoocoenosis," "biogeocoenosis," "biogeocoenology," and their derivatives, with meanings self-evident from their Greek roots, are perhaps the clearest and least misused terms in ecology. They perhaps could (or should) be substituted generally for their confused English equivalents, except that we should retain the easier term "ecosystem" (instead of biogeocoenosis).

Abstract versus Concrete Ecosystems

The ecosystem concept must be understood, in an abstract sense, as any biological community of one or more organisms plus, and interacting with, its environment. In this sense it would apply to any such system, from a single bacterial cell in a minute drop of water, to the earth with all of its organic inhabitants and all environmental entities that affect them. In its concrete sense, ecosystem applies to any particular spatial unit or stand with its included organisms and the environment with which they interact or by which they are affected. The problem of distinguishing between the abstract (type) and

the concrete (example) will be with us as we examine every level in the hierarchy of ecosystem classification.

Confusing Ecosystem and Vegetation Classifications

There has been an unbelievable amount of discussion and a plethora of publications on flora, "vegetation," animal communities and ecological concepts, and an attempt to describe and summarize them, if adequate, would require a book, rather than a review paper. By far the greater part of pertinent work on vegetation and ecosystem concepts and classifications has been done in local, or geographically restricted investigations, usually not claimed to be of more than local application. Some authors, however, assume a broader applicability than is warranted, extrapolating from local observations, making generalizations that apply less and less well the farther one goes from the area where the observations were made.

A considerable number of vegetation classifications have been proposed, described and applied, a few on a general or world scale, many more for restricted areas. A dichotomy has developed between those few classifications which are based strictly on plant or vegetational features, and those including in their definitions such environmental features as climate, soils, moisture, or even animals. In this paper, the term "vegetation" will only refer to the plant component of ecosystems being discussed. In this restricted sense, circularity of reasoning can be avoided. Vegetation cannot at the same time be defined by soil features and then be used to define or characterize soils, for example.

Granting this restriction, most so-called vegetation classifications and the maps based on them are really ecosystem classifications and ecosystem maps. Few vegetation students and mappers are willing to accept this restriction, and most continue to call their schemes vegetation systems and maps. The Engler and Drude (1902), Rübél (1930), Braun-Blanquet (1932), and Fosberg (1961a, 1961c, 1967) systems are the principal early schemes to truly or even primarily qualify as vegetation classification systems on a general or world scale.

PROBLEMS OF DEFINITION AND DELIMITATION

Before considering the existing classifications, it seems appropriate to discuss the problems encountered in defining and delimiting ecosystems as they have concrete existence in the field, and determining how, if possible, they may be related in a hierarchical system. One is intuitively aware, once one grasps the ecosystem concept, that ecosystems, in the concrete sense, exist as discrete entities.

It is no accident that there has been a great deal of description and classification of what has been considered as vegetation, i.e., plant cover. Vegetation can be seen and

its variations described and measured. The plant component is clearly the most tangible of the complex of features and qualities that make up most terrestrial ecosystems.

Ideally, of course, an ecosystem should be delimited by taking into account all of its components or attributes. But for practical reasons this is generally impossible. In practice, some of the components may be measured or defined in terms of other components. Soil surveying and mapping, after the reality of a soil type is established by actual sampling, are done by observing vegetation correlation with soils, and mapping the vegetation on the assumptions that the limits of the soil type are indicated by the boundaries or areal extent of the corresponding vegetation.

A first approximation of the extent and boundaries of an ecosystem may thus be established by discerning and mapping a vegetation feature or complex of features. This is the property of the ecosystem that is immediately visible and may possibly indicate the extent and boundaries of the ecosystem under study. If adequate spot-checking of other important but less obvious features or properties of the system (e.g., soils) establishes that the spatial extent of the vegetation corresponds with that of the corresponding ecosystem, we have a practical basis for placing it in a classification and determining the set of phenomena that we are interested in.

Inventories of Organisms

In characterizing an ecosystem at any level it would seem necessary to list or inventory two sets of phenomena - the biotic or living component - flora and fauna, and the inorganic environmental features. Neither of these enterprises is easy. On the organic side, such large and conspicuous animals as birds and mammals are fairly easy to identify and count. Likewise trees are large and obvious - witness the frequent inventories of plants (trees) 10 cm or more diameter at breast height. Shrubs, vines, and herbs are fairly easy, but often disregarded. But the cryptic, small or tiny organisms - earthworms, salamanders, insects, spiders, mites, nematodes, fungi, actinomycetes, protozoa, algae, and bacteria - that make up by far the greatest number of species in any natural ecosystem are a different matter altogether. To complete such an inventory requires either an old fashioned across-the-board naturalist or a team of specialists.

Inventories of Inorganic Features

Likewise, the inorganic components of an ecosystem (e.g., the soils, landforms, water) must be identified, measured, their ranges of variation determined, their synergistics and their effects on the living components understood and identified. Again, this is no mean array of tasks, but it is necessary if an ecosystem is to be fully understood as a functioning whole.

Use of Selected Features or Components

Clearly, to inventory and evaluate all organic and inorganic components of ecosystems to be classified would be totally impractical. No classification would ever be accomplished. What, then, is the alternative? It seems clear that a few important and readily observable attributes must be selected and assumed to be the parameters that define the ecosystems at any particular level in the hierarchy. Different such sets of features would be suitable at different levels, and an estimation of the breadth and importance of major features or sets of features would determine the levels and their order in the hierarchy. At least for the higher parts of the hierarchy, the science of biogeography should be enlisted to help select these criteria. To the best of our knowledge, this approach has not been tried, although some of the so-called vegetation classifications, those in which broad environmental, rather than strictly vegetation characteristics, are basic, may actually be the results of similar logic.

Biogeography

Biogeography may be thought to provide an approach to an ecosystem classification but there is so much difference of opinion as to what is biogeography that this confusion must be put in order before it will be very useful for anything of this sort. There seem to be at least four main subject-matters referred to as biogeography or its two subdivisions phytogeography and zoogeography (Fosberg 1976):

1. Floristic/faunistic biogeography, perhaps better called statistical biogeography, is perhaps what is most commonly meant by the term. In this, plant and animal species are sorted into groups called "elements" based on what are considered to be their closest taxonomic relationships. Then these groups are arranged geographically into "geographic elements." A preponderance of any one of these in a flora or fauna indicates its principal geographic affinity. This seems theoretically a sound approach, and is applied in many biogeographic studies and texts. However, the uneven and frequently inadequate taxonomic knowledge in many major groups of organisms and incompleteness of collection in many geographic areas lessens one's confidence in conclusions reached in this way.
2. Another major field of biogeography is called historical biogeography. This attempts to interpret and understand distributional patterns in terms of what is known of the fossil histories of faunas and floras, and of paleogeographic reconstructions. These approaches not only contribute to the development of a biogeographic picture of the biota of an area or region, but what is known of the biota helps fill in the paleogeography and the knowledge of the migration and evolution of the plant and animal groups and lines of descent (e.g., vicariance versus dispersal theories of biogeography (Udvardy 1981) or the "equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967)).

The results of these sorts of biohistorical speculations, correlations, and reconstructions are often combined with determination of the succession of strata. The apparent chronology provides materials for stratigraphic determination of the relative ages of strata and their included fossils. Then the presence of taxonomically similar fossils may be used to indicate the age of other strata in which these fossils occur. The lists of fossils of putatively similar ages are compiled into fossil floras and faunas. These may then be assumed to indicate paleo-ecosystems. However, there seems to be so much incompleteness and inherent uncertainty in the results of this approach that historical biogeography can scarcely contribute much to a practical ecosystem classification.

3. Economic biogeography is the collection and organization of information on useful plants and animals, and products derived from them in terms of their geographic origins and distributions. This is a special aspect of biogeography of considerable practical importance, but it has little pertinence to ecosystem definition and classification.
4. There remains the subject of ecological or physiological biogeography. This, the classical, or Schimperian biogeography, usually phytogeography, had its origin in Humboldt's observation of zonal distribution of organisms according to altitudinal belts in the Ecuadorian Andes (Humboldt 1805, 1806). It was launched as a formal science by A.F.W. Schimper in 1898, in his monumental "Pflanzengeographie Auf Physiologischer Grundlage" (first translated into English in 1903 by W. R. Fisher). This great work divides the land surfaces of the earth into plant-geographic regions on the basis of climate, temperature and rainfall regimes, soils, elevation, and other ecological factors, as expressed by the structure and physiognomy of the vegetation. On a world scale, this scheme resulted in a very coarse-grained pattern, but an eminently sound one. It is, of course, really an arrangement of major ecosystems, though commonly referred to as a vegetation system. Much work has been devoted to refinement and improvement of Schimper's essentially physiognomically definable and recognizable units. It has been given more attention by geographers than botanists or zoologists, but it is basically ecological. Schimper's regions and subdivisions are in reality major ecosystems based on complexes of ecological factors and recognizable from variations in physiognomy of vegetation. Modern refinements of these units will most likely form the higher levels of any hierarchical classification of ecosystems. As noted earlier in this paper, vegetation is the most visible feature of almost any major ecosystem and its nature and appearance provide the best indicators of the ecosystem extent and boundaries.

Aquatic Situations

Aquatic ecosystems do not fit well with much of what has been said above, which is mostly about dry-land or wet-land terrestrial phenomena. Large bodies of water, marine benthos, small lakes and ponds, streams and rivers, and flowing springs cannot ordinarily be identified and defined by readily visible vegetation. They certainly contain biotic communities in addition to their physical environments, but their environments provide water rather than soil and air as the medium or matrix. In some cases the vegetation is evident enough to be useful in defining the system, but in others we must depend on other features such as chemical or physical structure of the water medium. The water may be saline or fresh, acid or alkaline, clear or turbid, still or moving, smooth or turbulent, warm or cold, seasonally frozen or not, and more or less (usually more, these days) polluted. These features and combinations of them will influence or control the organic components of the system. An almost infinite number of combinations may occur. It seems clear that the whole natural range of ecosystems should be divided into terrestrial and aquatic segments, each of which would comprise a separate hierarchy in any complete hierarchical classification. It will be difficult to determine which of the sets of features listed above under the aquatic environment are useful to our purposes. Those pairs of attributes are not the only ones of significance, but seem to be the most important in order to provide bases for a usable hierarchy.

Succession and Continuous Variation

The problem of succession will have to be dealt with in both aquatic and terrestrial ecosystems. Clements (1902, 1928) has provided a rather clear framework in his hydrosere-halosere-xerosere terminology. His hydrosere is perhaps the easiest to visualize, though all too easy to oversimplify. Emergent aquatic vegetation, especially on tidally or other intermittently submerged and emerged ground (and continua), whether successional, non-successional, geographic or periodic, are realities to be dealt with. This is most especially true when our most basic discontinuity, that between aquatic and terrestrial ecosystems, breaks down. The truism that sharp boundaries are rare or non-existent in nature is nowhere more evident than here. Even the apparently sharpest boundaries are made fuzzy by "edge effects."

Diversity

A concept that has, to a few scientists, been of importance for a long time, has in the last few years been recognized to be of major consequence to a wide audience. Diversity has come to be recognized as a factor in the stability and permanence of major ecosystems. Such a subject, attracting more than just scientific attention, and now even of political consequence, is certain to stir up controversy. Even the definition of

diversity, once regarded as obvious, has become a matter of argument with some definitions so mathematical as not to be obvious at all.

A stated objective of many classifications is the preservation and protection of biological diversity. Diversity must therefore enter into the classification of ecosystems. What most organizations intend to preserve is actual diversity in terms of numbers of species. These are essential components of functioning ecosystems, clear and simple enough to be readily understood by educated and intelligent people, and not only by specialists in technical ecology.

While the objective is the preservation of the mosaic of complex communities of interacting organisms, the habitats that are home to the diverse multitudes of species are equally diverse. The geological base may be of many kinds, physical and chemical, of rocks, the parent materials for a diversity of soils. Erosion and tectonic uplift of these, and volcanic outpouring from the complex series of magmas forming and combining beneath the surface of the earth, and the erosion and weathering of surface rocks provide a rich diversity of habitats for the multitude of plant species that provide habitats for the diversity of animals. All of this adds up to a remarkable physical diversity and a much greater biological diversity or "biodiversity," all of which we must do everything possible to preserve.

Virtually every aspect of the intricate web of biotic and inorganic diversity provides an ecological niche that supports one or more species of plants or animals. Each such community which interacts within itself and with its segment of habitat, forms a definable ecosystem. Such ecosystems, at every level of complexity, are what must be ordered and classified so that knowledge about them is made accessible. The resulting classification must serve as a guide to this labyrinthine complexity.

EXISTING SCHEMES OF CLASSIFICATION

As noted above, there is an enormous literature on classification of vegetation, animal communities, ecosystems and, in general, ecological entities. As also mentioned, it would require several books rather than a review paper to digest and summarize this literature. A plethora of terms, maps, and systems have been proposed, and many of these are, or have been, in use. Many of them have value, especially in relation to the purposes for which they were created. Some of these purposes and values are discrepant and even conflicting. No one system of ecological terminology or classification is suitable for all purposes. This view is not, however held by all workers in the field. The extreme opposite position was very positively expressed by no less a person than Professor van Steenis who said (1956 conversation with Fosberg), "there can only be one correct vegetation map of an area."

In this paper it seems only practical to give an idea of the principal systems of very broad, or worldwide application; and of terms and concepts of possible use or significance in formulating a hierarchical classification of ecosystems for use in efforts toward conservation of biodiversity, especially in the Pacific islands. No special effort is being made to be sure of the complete history of a term or even of a system, so long as the concepts are clear and understandable. More attention will be paid to the appropriateness of terms, concepts, and features of the systems discussed for use in the classification to be constructed. A basic aim will be to determine and convey how effective a term or concept will be for storing and retrieving information for the proposed classification of ecosystems. This objective may in places cause the sequence of this paper to be less direct or economical than might be expected.

It is not our purpose here to describe the ecosystems that are classified, but we may properly be reminded that no matter how good a classification is, the results of its use or application will be no better than the quality of the records of the ecosystems, or communities plus environments, to be classified. The recording and description of data on the natural phenomena of vegetation is a whole other subject, but an important and essential one (see Dansereau 1957). Terminology is the connecting link between the descriptive data and the classification, so terminology will frequently be discussed and used in the remainder of this paper. Some definitions will be offered of terms that are not obvious.

We will present three general types of classification schemes. These are:

1. Strict or almost strict vegetation classifications;
2. Ecological approaches to vegetation classifications; and
3. Ecosystem classifications.

Some of the systems discussed in these three sections will be discussed again or referenced during the later presentation of classification units. A later section also covers systems of biogeographic classification as a possible approach to the top level in a classification of ecosystems.

Strict or Almost Strict Vegetation Classifications

The Braun-Blanquet System of Phytosociology: The most widely accepted vegetation scheme, especially in continental Europe, is that developed by Professor J. Braun-Blanquet of Montpellier, France, and associated also with Zurich, Switzerland (Braun-Blanquet 1932, English translation by Fuller and Conard; also see Becking 1957). The Braun-Blanquet system of vegetation science, though usually thought of by those not involved with it as just a scheme of classification, and nomenclature, is actually a well-rounded method of collecting, organizing, and interpreting information on plant cover

of areas of the earth's surface. It is only the classification aspect that concerns us here and that most Americans are aware of.

The Braun-Blanquet approach is based on floristic data, which are used as indicators of the associations, the basic unit, and of higher units which are groups of associations. The data for these higher units indicate but are not based on environmental factors. This differs from the usual American indicator concept (e.g., Clements 1902, 1936) in that it does not hold that a single species reliably indicates an environmental complex, but that a number of species together give a more reliable indication. The concept of "fidelity," that certain species are found in no other "association" is central to the system. These faithful species are called "character species." Other species, present, but not exclusively so, are called "constant." A group of species usually found together in the association, and useful in differentiating it from other associations, are called "differential species." The procedure of the method, after the selection of the plots, on which the "relevés," or working building blocks of the system are selected, is a prescribed standard order which, if followed, will yield associations, if such exist in the area of vegetation.

The critical operation in Braun-Blanquet's method is the choice of plots for making the relevés on which the floristic analyses are based. A standard sized area of homogeneous vegetation is chosen subjectively. The data which are abstracted from these plots are the raw material from which the relevés are compiled. The relevés are then tabulated and the associations are derived statistically from the tables. One of the most severe criticisms of the system has been aimed at the subjective, rather than random choice of plots. In our opinion, the careful selection of plots, based on experience with the vegetation is the real strength of the method. If the choice of plots were random, it would be very unlikely that any associations would result from the operation. The association, as stated above, is the fundamental vegetation unit of the system.

These associations are grouped into a higher category called "alliances," by the same method, and the alliances into orders, and the orders into classes. The associations are usually not readily recognizable on quick ground observation, and reading a description of vegetation according to this system gives no visual impression of the vegetation. At the alliance level it is often possible to recognize the units visually in the field, but only after some experience.

The Braun-Blanquet scheme undoubtedly detects and portrays something real, and maps based on it have proven very useful in indicating environmental factors and in land-use planning. However, it is not clear that it would help in defining ecosystems, at least not without a high cost in time and labor. In spite of its wide acceptance, we can ignore it in our present context. We have described it in some detail, informally, because it is so firmly entrenched in the science of phytosociology that strong arguments are possible for its adaptation as the basis for the description of the vegetation component of the

ecosystems to be classified. Though a useful scheme, we do not at all recommend it for our purposes (also see Egler 1954).

Dansereau's Scheme: Another system, completely structural and based on features of the plants only, was proposed by Dansereau (1957, 1958). Basic in this system are six features: (a) plant life form (after Raunkiaer 1937), (b) plant size, (c) coverage [%], (d) function (deciduous or evergreen), (e) leaf shape and size, and (f) leaf texture. Each of these is subdivided, the divisions represented by letter symbols. These criteria can be combined to indicate formations. The system is more precise than a strictly physiognomic one, and when used for mapping, can be supplemented by profile diagrams according to Dansereau's (1958, pp. 31-72) formal or symbolic system. The system is useful, and our only objections to it are the use of letter symbols and percentages for cover, and that it does not cover a sufficient range of variables.

Also interesting is Dansereau's (1957, pp 128-131) digest and illustration of del Villar's (1929) ideas, basic to critical consideration of ecosystems. Dansereau's short summary makes it clear that this is an important work, and should be considered by anyone seriously interested in the ecosystem concept.

Küchler's System: Küchler (1949, 1967, 1972) has proposed a structured hierarchical system that accounts for an ample range of observable variables. He calls it a "physiognomic classification," but it is much more than that. It is structural and also functional in Fosberg's sense (see below), and it is very suitable for mapping, if a legend is provided. Our main objection is that it is expressed in letter symbols and formulae rather than names and diagnoses, therefore giving no visual impression of the vegetation. His main subdivision is into woody versus herbaceous. This presents inherent difficulties in dealing with massive succulents and other acaulescent xerophytes, giant herbs such as Musaceae (sensu stricto), and lianas or climbers. This scheme or a modification of it may well be useful in our discussions.

Fosberg's Scheme: In the 1950's, Fosberg's studies of tropical island vegetation directed his attention to possibly appropriate terminologies and classifications to use in placing on record the vegetation information acquired. Most of the existing systems had been developed in the temperate zones and were less well-suited to tropical vegetation. Most systems also involved environmental features, especially climate, soils, and available water, in addition to or even in place of the vegetation itself.

Fosberg experimented with possible methods of using only features of the plants and vegetation. Over several years he developed versions of a scheme utilizing what he called "structural and functional features" of the vegetation (1961a, 1961c, 1967). The difficulties were apparent in dealing with aquatic vegetation and terrestrial vegetation in extreme situations such as on cliffs and in deserts. Environmental implications crept in, especially into the terminology. A final version of this classification was included in IBP

Handbook No. 4, of the IBP section of Conservation of Terrestrial Biological Communities (Fosberg 1967).

The primary subdivision in this system is the spacing of the plants, i.e., closed, open, or sparse. Spacing is estimated by a visual method not involving percentage cover. The three units at this level are called "primary structural groups." Under these are "formation classes" and in these, "formation groups." The basic category, then, is the "formation" under which there may be "subformations" if needed. The classification goes no further, as any further subdivisions would be on floristic composition, which is impractical on a world-wide scale.

Fosberg attempted to construct a classification that will work where only a minimum of information is available, but which is adaptable and capable of further subdivision by using modifiers with the terms when more adequate information becomes available. Fosberg avoided the term "cover" in its usual sense, as it implies the (usually impractical) measurement and determination of percentages. He also avoided floristic information, though that can be added in a modifier sense. Floristic information is mostly useful in establishing "associations" which form a lower level than Fosberg's classification includes. Finally, he also avoided terms which end in "land," as these imply habitat and are broader than a strictly vegetation sense. This suffix may well be added to convert higher level vegetation units into ecosystem units, e.g., grassland, woodland, shrubland, etc.

The Fosberg system has been compared with the UNESCO (1973) classification by Goldsmith (1974) showing that each has its advantages and weaknesses. It should be noted that Eiten (1968) has developed and proposed a major revision and amplification of the Fosberg classification, resulting from his extensive experience in Brazil. He has introduced much detail and more precision. Anyone proposing to use Fosberg's system for more than casual vegetation work would do well to give serious attention to Eiten's paper.

The USFWS Structural Classification: A new and very different classification has been proposed by the USFWS prepared at the Thorne Ecology Institute, Boulder, Colorado, available in duplicated form only (Moir *et al.* 1988). It is a classification of terrestrial vegetation, based on structural features only. It is supposed to be a step forward from the Dansereau, Küchler, and Fosberg schemes, especially suitable for temperate zone vegetation, and easier to use by workers with little or no botanical knowledge. The aim of the authors was "to produce a structural classification of terrestrial vegetation with particular application to North America, but also intended to apply worldwide."

The authors have abandoned names for their units, below the top rank of "major structural groups," of which there are eight: forest, woodland, scrub, dwarf scrub, herbaceous vegetation, nonvascular plant vegetation, and barren. These are defined

mainly by percentages of different growth-forms. They are subdivided into up to 10 different defined "ranks," designated by numbers, modified by "descriptors" or characters of vegetation structure. "A descriptor is a class of objects that exist in discrete conditions. Each descriptor has been partitioned into mutually exclusive subclasses, or "states." Each state has a letter code followed by a word or "phrase."

A glossary is provided, which gives special, often lengthy, frequently unfamiliar, definitions for most of the important words used in the classification and text. The user will get nowhere until he has thoroughly familiarized himself with this glossary. A list of references cited is given, with familiar and unfamiliar authors and papers, also with surprising omissions.

This work seems to be an almost total departure from traditional vegetation concepts and classifications. There is no doubt that if properly applied, a useful and valuable mass of information on vegetation would be accumulated. One would not know what to call the units. Many definitions are in terms of percentages, perhaps giving a false sense of precision. Special uses of familiar terms create confusion.

One item Moir *et al.* bring out in their introduction is the fact, usually neglected or ignored, that standing and fallen dead trees, rotting logs, and other dead remains are still part of the vegetation. This is a somewhat controversial matter, though Fosberg has long agreed with it, particularly concerning peat and mor. Dead material is certainly an important part of the ecosystem.

Our comment on this classification is that it is an interesting departure, but that it is not likely to contribute much toward the task of arriving at a suitable classification of ecosystems.

Ecological Approaches to Vegetation Classifications

The systems reviewed above are more-or-less true vegetation classifications, the features used as criteria being those of the plants - the plant species or the plant aggregations. Only a few classifications come even close to resting on plant characters only. With only one exception (Braun-Blanquet) among the systems examined, environmental features have crept in, especially in defining units of vegetation in extreme habitats. Most self-styled vegetation classifications are based partly on environmental phenomena. Many of these are perfectly sound systems, but must be regarded as ecosystem rather than vegetation classifications, since they include both organisms and their environments.

It is hard to say who started to classify vegetation in terms of the ecological factors that theoretically control its form and distribution. Grisebach (1872) is said to have established the "formation" category, basic in most physiognomic and structural systems. His book was on the role of climate in classification of vegetation, and it had

much to do with the direction of subsequent work. Schimper (1898) firmly established this tradition (see below) which has dominated much of the non-Braun-Blanquet vegetation study, and probably should be referred to as "geobotany."

In earlier pages we have commented on the use of vegetation in establishing the spatial or geographic limits or boundaries of natural, especially major, ecosystems. We can only summarize some of the high points and mention several important works in the vast literature on geobotany or ecological vegetation study, but must point out that this work is basic in what we are working on, no matter whether the subject matter is called "vegetation" or "ecosystems." It is a pity that so many of the important works are in German, making it hard work for us linguistic semi-literates to read. Fortunately a few of these, especially Schimper, have been translated.

Schimper's System: Schimper (1898) devoted the greater part of his huge book to details of the ecological, geographic, and especially climatic relations of vegetation on earth. Little that was known in these fields in his time was neglected by him. Even now, almost a century later, there are many days of profitable reading in Schimper's big book for anyone with ecological interests.

For our purposes his Part II, Chapter 1, on Formations and Guilds, is most pertinent. He groups vegetation into three vast categories: woodland, grassland and desert. Already he has established that he is writing about ecosystems, though the term and the concept had not yet been invented. Those three groups of formations he believes are due to regional climate. Subordinate to his climatic formations, he proposes "edaphic formations" due to "differences in the physical and chemical nature of the soil." His discussions in this chapter occasionally sound quite anthropomorphic, as he is clearly trying to show a large and probably unscientific audience his conclusions. He proposes, or uses, many terms which have become well-established in ecological parlance, e.g., xerophyte, lithophyte, chasmophyte, psammophyte, etc.

Schimper, although he did much to establish the formation concept, and provided great amounts of description of formations, did not systematically classify and characterize his formations. He had too much fascinating information about them to settle down to organization and routine description. He left that to his numerous, mostly German and Swiss followers. He was obviously much more interested in the remarkable phenomena that he observed and interpreted than in classification and terminology.

Schimper's Successors: Von Faber, co-author of the great third edition of Schimper's book (Schimper and von Faber 1935), organized the formations into 15 "formation types" (termed formation classes earlier by Rübel (1930) and also by most subsequent authors), and prepared a world map of these, redrawn later by Dansereau (1957). Rübel recognized only nine formation classes; Dansereau, following Schimper and von Faber, recognized 15; Küchler 32, Fosberg 31, and Schmithüsen eight with many subclasses. These are clearly not really comparable or equivalent.

Schmithüsen (1968) gathered an enormous compilation and interpretation of the "vegetation" information that has any geographic or landscape interest. This major work summarizes the geographic and ecological information available in his time, albeit in complicated German. It is far too detailed to even summarize here, or for our purposes, but will, for a long time, be the major reference in what we are calling geobotany, as well as in much of ecology.

The UNESCO Classification: In 1969, a physiognomic classification of world "vegetation" was published, prepared under the auspices of the UNESCO Standing Committee on Classification and Mapping of Vegetation on a World Basis (UNESCO 1969). This, as with so many other "vegetation" classification and mapping schemes, was not strictly based on vegetation features, but included environmental criteria, and must, on a strictly logical basis, be called an "ecosystem classification." This system was revised and republished in 1973 by Heinz Ellenberg and Dieter Mueller-Dombois as International Classification and Mapping of Vegetation (UNESCO 1973), and is sometimes referred to as the Ellenberg or Ellenberg and Mueller-Dombois system (e.g., Goldsmith 1974).

This is a hierarchical scheme with units in five levels of subdivision: formation class, formation subclass, formation group, formation, and subformation with provisions for further subdivisions where necessary. Its first subdivision, on the basis of stature and spacing, divides vegetation into five formation classes:

- I. Closed Forest;
- II. Woodland;
- III. Scrub;
- IV. Dwarf Scrub and related communities; and
- V. Herbaceous Vegetation.

Each of these, and its subdivisions at four or more levels, is given a phrase name and/or a diagnosis, separating it from its related coordinate units. The criteria used are, where convenient, such features as evergreen or deciduous leaves, growth form, leaf shape and texture, and such environmental features as altitude, dryness, seasonal rhythms, habitat, and whatever may help to recognize or distinguish the units. In many cases, examples are added which help greatly in visualizing the units. Each unit described is given a serial numerical designation and a distinct formula (e.g., II.A.2.a.(1) following traditional outline format). The example code indicates "Evergreen needle-leaved woodland with rounded crowns with evergreen sclerophyllous understory."

This is not perfect, but it seems to be the most satisfactory terrestrial ecosystem classification yet proposed. It is included in essentially its original form in the Mueller-Dombois and Ellenberg volume on vegetation ecology (1974).

The IUCN Classification: In the same year (1973) that the UNESCO scheme appeared, IUCN published "A Working System for Classification of World Vegetation," which is a simplified and shortened version of the UNESCO effort. It uses a more familiar, vernacular terminology for naming its units, and combines some similar units from the UNESCO system. It is really three parallel classifications, one for tropical and subtropical vegetation, one for humid and sub-humid temperate and sub-polar regions, and another for deserts, sub-deserts, wetlands, and aquatic formations. This scheme is undoubtedly easier to use in the field, and for most purposes is satisfactory, though not designed to record as much detail as its parent UNESCO system. It does not provide for the more minor floristic systems at the association level and lower, a shortcoming shared almost by definition with every other world scheme except that of Braun-Blanquet.

Daubenmire's System: In 1978, R. Daubenmire proposed a system of plant biogeographic regions for North America. His system begins with biogeographic regions based on climatic vegetation climaxes. The next level is the "province" within which geologic history is relatively uniform and plant taxa are historically related. The next level is the "zone" within which macroclimate and soil groups are generally uniform. Finally, the fourth level is "habitat type" based on potential natural vegetation.

Ecosystems Classifications

Since the concept of "ecosystem" is a relatively new one, and one that for years has either been widely ignored or misunderstood, only a few classifications of these systems per se have been developed. A few of these will be briefly considered here, including the earliest, by A. B. Klugh, and later efforts by V. Krajina, and H. Ellenberg. We will also introduce two wetland ecosystems classification systems, and finally, give a brief account of the classification challenge of subterranean ecosystems.

Klugh's System: In 1923, A. B. Klugh briefly reviewed the subject of ecological classification and proposed a "Common System of Classification for Plant and Animal Ecology." This scheme which includes marine, fresh-water and terrestrial ecosystems depends almost entirely on environmental criteria, seems one of the best attempts to classify habitats of both plants and animals. It is rather general for our purposes, but deserves serious consideration. It has not been widely used, possibly because it introduces and uses many new or totally unfamiliar terms. It does account for practically every existing ecological situation that was known in 1923.

Krajina's System of Biogeoclimatic Zones: Working on the ecology of British Columbia, Professor Krajina (1965) designed a system of what he termed "biogeoclimatic zones" (Mueller-Dombois and Ellenberg 1974, pp. 166-168). He defined a biogeoclimatic zone as a geographic area that is predominantly controlled by the same

macroclimate and characterized by the same soils and same zonal (climatic climax) vegetation.

The term "zone" which is common in the literature of soils and, to some extent, of vegetation, is elusive, varying somewhat with the particular writer. It seems generally to imply a geographical phenomenon controlled by limiting habitat factors. When these vary continuously, local phenomena of vegetation or animal community belts (along altitude, moisture, or other gradients) may develop (e.g., Holdridge 1947, 1967). When these factors vary discontinuously, a mosaic of zones may develop. While the former type is typically fairly small, the latter may be quite large as in Krajina's system.

Krajina included within his biogeoclimatic zones the biogeocoenoses of Sukachev. The aerial extent of a biogeocoenosis is determined by the extent of the phytocoenosis, which is a rather narrowly defined and mappable plant community. Krajina's system is very useful for the study of major ecosystems. Its main advantage and obstacle to application is the diversity of data that must be collected to classify its ecosystems. This range of data is not ordinarily within the competence of an individual ecologist.

Ellenberg's Classification of World Ecosystems: H. Ellenberg (1973), based on a lifetime of experience as an ecologist, proposed a comprehensive, hierarchical scheme for world ecosystem classification including phenomena and concepts that, though obvious and important, have rarely been included in other classifications (e.g., the influence of human activities).

The hierarchy starts at the top with the all-encompassing world ecosystem, or "biosphere." This is subdivided partly on the basis of the energy sources utilized: the sun for natural or predominantly natural ecosystems; and "reconstituted energy" or fossil fuel or atomic energy for "urban-industrial" ecosystems. Note that a modern system would have to include the chemical energy-based natural ecosystems of the oceanic thermal vents. Another criterion used by Ellenberg is the life medium. This second level includes five divisions or "mega-ecosystems." These are marine (salt water), limnic (fresh water), semi-terrestrial (wet soil and air), terrestrial (aerated soil and air), and urban-industrial (human-created) ecosystems (including agro-ecosystems?).

"Macro-ecosystems," the next level, are based on productivity - consumer - decomposer phenomena and the factors regulating these processes. "Meso-ecosystems" make up the next level, and are considered the most basic units of the scheme. A meso-ecosystem is composed of a relatively uniform or homogeneous abiotic system plus its characteristic life forms functioning as primary and secondary producers. "Micro-ecosystems," the next level of division, are characterized by distinguishing natural features or life-forms. Each "nano-ecosystem," at the next level, is unique, and is characterized by its particular natural features and species.

The definitions of the units at each level in the terrestrial branch of the hierarchy are characterized primarily by vegetation according to the UNESCO structural-ecological formation system (UNESCO 1973), so the meso- and micro-ecosystems correspond more-or-less to vegetation formations and sub-formations. Ancillary subsystems at the various levels form a part of Ellenberg's overall scheme, but are not part of the hierarchy. These subsystems allow for additional refinement of ecosystem data. A category of subsystems such as layers, resource-sharing groups (*synusiae* or guilds), substrate inclusions, and "pheno-partial" or seasonal manifestations is provided for use at the meso- and micro-ecosystems levels. Another category of subsystems operating at the top level provides for identification of nine biogeographic regions, facilitating world-wide comparisons of lower level units. Still another set of subsystems is a scale of four levels or degrees of human interference with natural ecosystems. These include:

1. Harvesting of organic materials or minerals that are significant for the functioning of the ecosystem;
2. Adding organic or inorganic materials to the ecosystem;
3. Toxification, or adding substances to the ecosystem that are deleterious to its functioning or to that of its important component organisms; and
4. Changing the species composition by suppressing or causing the extirpation or extinction of existing species or by the introduction of alien species to the ecosystem.

This Ellenberg scheme is based entirely on structural and functional characteristics. Its usefulness obviously is proportional to the thoroughness with which an ecosystem or system of ecosystems can be described. As the most fully elaborated system for classifying ecosystems, it should be seriously discussed in any effort to develop a scheme for the classification of ecosystems. Its utility for conservation evaluation should be apparent.

The USDA Forest Service "Digitized" System: One of the strangest ecosystem classifications recently proposed was offered by Brown *et al.* in 1980. This system is intended to allow the USDA Forest Service to computerize information about ecosystems classified in a hierarchical way. The system begins with "biogeographic realms" (after Wallace and Udvardy) at the top level, and descends through "vegetation" (actually substrate) characterized by topographic position and available water, to formation type (e.g., grassland), then to climatic zone (potential natural vegetation), then to biome (apparently in the sense of sub-formation), and climax series (plant growth-form), in that order. This hierarchy scarcely seems hierarchical, or for that matter, sensible.

Wetland (Wet-terrestrial) Systems

The USDI Fish and Wildlife Service Wetlands Scheme: The USDI Fish and Wildlife Service (USFWS) must cope with the difficulties of classifying aquatic or

wetland habitats. That organization is required to maintain an inventory of the wetland resources of the United States. This was first established according to a scheme set up by Martin *et al.* (1953) that was relatively simple, but not altogether internally consistent nor complete. This scheme was created to be used as the basis for inventory and analysis of wildlife habitats.

Recently, the great importance of wetlands began to be realized, even by the intelligent lay public, and the necessity for a new and up-to-date inventory of wetlands *per se* became evident. The old paper by Martin *et al.* (1953) was no longer considered adequate for a proposed inventory, so the USFWS Office of Biological Services set up a project under Lewis M. Cowardin, who with three colleagues, Virginia Carter, Francis C. Golet and Edward T. LaRoe, undertook to produce a classification that would serve all of the agency's purposes. This was first published in 1977 and somewhat revised and reprinted in 1979 and 1985. It has been officially adopted by the USFWS and other US federal agencies for all of their wetlands classification, inventory, and regulation activities.

Cowardin *et al.* (1985) produced a classification of wetlands that accounts for almost every imaginable saturated or seasonally saturated environment. Applied properly, each unit can be described in almost every significant detail. The problem of assigning names to the units is avoided completely. All are called "wetlands" with a series of refining and modifying terms or codes.

The most obvious first breakdown might be between wetlands and deep-water habitats, but this separation does not enter the classification. The highest level in the classification is a series of five "systems" based on the character and occurrence of the water in each system. There are marine, estuarine, riverine, lacustrine, and palustrine systems. In other words, there are oceans; estuaries; rivers and streams; lakes and ponds; and swamps, bogs, and marshes. Ten "subsystems" form the next level based on water level and tidal behavior and the permanence of saturation. A still lower level of "classes" (one to eight per subsystem) is based on the nature of the bottom and on the biota. Classes may be further modified by additional codes for appropriate features.

As stated above, this scheme can account for any imaginable saturated situation. Many of the units have no defining biological characteristics, though microorganisms and cryptic forms are doubtless present. The units at all levels can be considered to be ecosystems and might be useful in our attempt at classification except that there seems to be no simple way to refer to them (a common problem of many of the schemes discussed here).

Some of the systems of wetland classification that this scheme was created to replace were much simpler and had named units, but the problem was that they did not account for all of the kinds of wetland ecosystems. The choice, as often happens, is between the simple and inadequate and the complex and impractical. The Cowardin

system and its predecessor were set up to take inventory of US wetlands. For our purposes, a selection might be made of aquatic ecosystems that include different biotas and that occur on islands. Whatever scheme is tried, it will not be both simple and adequate.

The Canadian Wetland System: Another wetland classification system has been proposed for use in Canada (Zoltai *et al.* 1975). This system utilizes only three levels. The first of these is "class," which seems to be based on vernacular formations (e.g., bog, marsh). The second level is "form," which has to do with the surface morphology of the wetland, soil type, acidity, water table position, etc. Finally, the "wetland type" is characterized by the physiognomy of dominant plant species.

Subterranean Ecosystems: A review of the literature on caves and subterranean ecosystems failed to yield anything like a comprehensive approach to cave ecosystem classification. Sweeting (1973, p. 158) classified karst caves as phreatic (above the water table, basically dry), vadose (caves containing running and/or standing water but not submerged), and vertical. Ford and Williams (1989, p. 243) listed thirteen factors for the classification of caves including size, shape (3 variations), relation to water table, rock type, mode of geological control, topographic setting (2 variations), role in the fluvial system of the region, porosity of the aquifer, relative activity of development (active *versus* relict), and climate. No classification of caves in igneous or metamorphic rocks nor of caves in tropical karst landscapes was encountered.

Under the circumstances, we might choose a few factors, perhaps to include rock type (limestone, other sedimentary rocks, basalt, andesite, other igneous rocks, metamorphic rocks), water type (salt, fresh, coastal mixing), water regime for fresh water caves (e.g., xeric and mesic in the phreatic zone, vadose) and topographic setting (e.g., montane, coastal, lowland, makatea) as an experimental basis for classifying caves.

MAJOR REVIEWS

We should not end this part of our account without mentioning, again, a few major reviews that bring together at least a substantial selection of the literature that has grown up around vegetation. Vegetation is an omnipresent phenomenon, so complex that no one completely understands all of its aspects. It is naturally excessively written about.

Schmithüsen's book on geobotanical classification, described above, gives one the feeling he would get from reading a street and business directory of New York City. One is amazed that anyone could have a grasp of such a labyrinthine collection of facts, and make sense of it, as Schmithüsen has.

On a more modest scale, but impressive none-the-less, are sections in two books. Mueller-Dombois and Ellenberg (1974) have effectively summarized many of the

principal vegetation classifications, bringing together in an organized and readable fashion much of what the ecologist or vegetation scientist needs to know. Dansereau (1957) has done the same in a different manner, interpreting principal aspects of plant geography in ecological terms and principles. These two books should be an essential part of the training of any aspiring vegetation scientist. Also see Shimwell (1972).

Animal communities, too, have received much attention, but less of this topic has been treated as generally as have plant communities. Most attention by zoologists and animal ecologists has been to what botanists call "autecology" - the behavior and ecological relationships of individual species, and particular relations between species. The range of interrelationships among animals has been written about, but is more elusive, the communities are less tangible, and the individuals sometimes run away and hide.

An outstanding attempt to generalize the animal aspect is the book on animal communities by L.R. Dice (1952). He wrote with great understanding in a wide field, but one does not get the feeling of being overwhelmed by the mass of information as one does in reading comparable works on vegetation.

Perhaps the most comprehensive reviews of biotic communities in English are Whittaker's 1962 and 1975 summaries of what is known of natural communities. These are truly comprehensive, organized, clear presentations of a tremendously complex subject. They tend to be more satisfactory on the vegetation side, being written by a botanist, but their frameworks integrate both major branches of community science.

CLASSIFICATION UNITS FOR ECOSYSTEMS

Some attention must now be paid to the nature and terminology of the ecosystem units to be classified and their levels in the hierarchy. Selection of designations for units is complicated by the necessity, in our ecosystem classification, to use terms for biotic communities, that is, those including both plants and animals. Terminology of plant or animal communities is usually available, especially for the former; in fact some feel that plant ecology is overburdened by its vocabulary. But terms for different levels of biotic communities, especially unambiguous ones, are less easy to find.

The term "community" itself, unqualified, should be defined without ambiguity. It should ideally mean an aggregation of interacting or interdependent organisms occupying a habitat. It has been much more frequently used for plants only or animals only, so perhaps where it makes any difference, the term "biotic community" should be used.

At the highest level of generalization, which also comprises the broadest geographical areas, there is easiest and most general agreement. This divides the earth's

surface into land and water (some of it frozen), coordinate with the aquatic and terrestrial divisions of the globe's surface.. There seems to have been little problem of controversy here, except on the boundary zones between the two. Some land is periodically dry or inundated. This and the land where the emergent plants are rooted below water level, are by different schemes included as either land or water. By some authors these are separated out into a catch-basket called Azonal.

Conceptual Discussion of Levels in the Hierarchy of Ecosystem Classes

An endless series of terms have been proposed and used to designate the kinds of units and the ranks or levels in which they are placed in classifications and mapping systems. Some of them may be appropriate for our purposes, but the great majority must be ignored, lest they lead to book-length discussions. We discuss a few of the most important ones. We will begin with a review of some of the more important biogeographic regionalizations. We will then consider the following: biomes, formation classes, formations, subformations, and associations, which are abstract (type or collective) terms. Concrete (actual) ecosystems may be called biomes, communities, associations, societies, regional communities, stands (ecotopes), and microstands. Distinguishing between terminology for types and actual occurrences is critical. We will recommend resolutions for the dual usages of "biome" and "association."

Major Biogeographic units

Biogeographers generally subdivide the terrestrial areas of the earth into major divisions, the names and boundaries of which have varied enormously according to different authors, from Schimper, Wallace, and Humboldt (the founder of biogeography) to Dansereau, Udvardy, and Bailey, among the most recent authors of world-wide systems.

Humboldt proposed the first scientific set of biogeographic regions based on the distribution of physiognomic vegetation formations controlled by climate (1805, 1806). We have already discussed Schimper's (1898) vegetation regions. In 1876, Wallace proposed the first scheme of zoogeographic regions, based primarily on Humboldt's work. Wallace intended to further develop his system on the basis of animal interactions with their environments, but he could not fully develop this idea with the data available, so he developed a system of natural regions based on the origins and extents of animal distributions (and in the process invented a new field of biogeography) (Rotramel 1973).

Udvardy's Biogeographic Provinces: Udvardy (1975, 1984), elaborating on Dasmann's (1973, 1974) tentative scheme, divided the terrestrial part of the earth into eight zoogeographic "realms" each subdivided into "biogeographic provinces." The Oceanian Realm includes the Papuan, Micronesian, Hawaiian, Southeastern Polynesian,

Central Polynesian, New Caledonian, and East Melanesian Biogeographic Provinces. He is presently working on a complete revision and elaboration of his 1975/1984 system.

Takhtajan's Floristic Regions: Takhtajan (1986) published a volume on the Floristic Regions of the World considerably updating the older system by R. D. Good (1947, 1964) which included four levels - kingdom, sub-kingdom, region, and province). Takhtajan divided the earth's surface into six kingdoms (e.g., the Paleotropical Kingdom), several subkingdoms (e.g., the African, Madagascan, Indomalesian, Polynesian, and Neocaledonian Subkingdoms in Paleotropis) and 35 floristic regions. In the Pacific, these include the Malesian, Fijian, Polynesian, Hawaiian, and Neocaledonian Regions in both the Indomalesian and Polynesian Subkingdoms. Regions may be subdivided into subregions (e.g., the Malesian and Papuan Subregions in the Malesian Region), and all regions (or subregions) are then subdivided into provinces (e.g., the Celebesian, Moluccan, Papuan, and Bismarckian Provinces in the Papuan Subregion).

Dansereau's Biochores: The most inclusive major unit that might be considered an ecosystem is the "biochore," as treated by Dansereau (1957), which is based on a combination of climatic factors and very general structural features of the vegetation. Each biochore includes a number of "formation classes" (*sensu* Rübel 1930) (equivalent to the formation types of Schimper and von Faber 1935). Although the biochore concept has not been widely used, it seems to be a real high-level ecosystem, and of great interest.

Bailey's Ecoregions: For a number of years, R. G. Bailey of the USDA Forest Service has been working toward a system of "ecoregions." Bailey's Ecoregions of the United States was published in 1976 (map) and 1980 (descriptions) (and revised by Omernik in 1987). In 1986, Bailey and Hogg published a prospectus for "A World Ecoregions Map for Resource Reporting," and in 1989, Bailey published his Ecoregions of the Continents. An ecoregions map of the oceans is in development.

These ecoregions are based on climate (after Köppen 1923, 1936 and Thornthwaite 1933) and vegetation, broken down in various ways, and applied in such a way that areas with various features form correlated wholes. Four hierarchical levels are recognized. At the top are the Polar, Humid Temperate, Dry, and Humid Tropical Domains. The domains are subdivided into 15 primarily climatic "divisions," in each of which there may be either one or two "regimes" (mountains and/or lowlands). The divisions (and regimes) are subdivided into ecoregions on the basis of vegetation, of which there are 101 on the terrestrial surface of the earth.

Whether these ecoregions are intended to be equivalent to biomes (discussion below) is not altogether clear; but the subdivisions result in more ecoregions than there are generally recognized biomes. There is little doubt that Bailey's and Omernik's ecoregions are natural, very large ecosystems. They should be considered in any essay toward the classification of ecosystems.

Biogeographic Units in the Pacific

Four authors have published biological or ecological regionalizations of the insular tropical Pacific. Three of these are based more-or-less on flora and vegetation (Fosberg 1957a, 1957b), birds (Mayr 1940), or terrestrial animals (Curry-Lindahl 1980a, 1980b). Only one deliberately includes environmental factors. Dahl (1980) includes island form and origin and climate as well as distribution of species and communities. The insular segregation of these units precludes considering them as large scale ecosystems, unless the marine components are considered and discovered to provide system-wide connections.

Mayr's Polynesian Region: At the sixth Pacific Congress (Berkeley 1939), Mayr presented a paper entitled "Borders and Subdivisions of the Polynesian Region Based on our Knowledge of the Distribution of Birds" (Mayr 1940). Mayr defined the Polynesian Region as the tropical islands of the Central Pacific east of the Philippines and Japan, west of the Galapagos, and north of New Zealand. New Guinea is considered to be a separate subregion, leaving a Polynesian subregion including the following divisions: Micronesia, Central Polynesia (west of 165° W. longitude through Fiji), Eastern Polynesia (east of 165° W. longitude), and Southern Melanesia (Santa Cruz and Banks groups, New Hebrides, Loyalty Islands, and New Caledonia).

Fosberg's Vegetation Provinces of the Pacific: In 1953, Fosberg presented a characterization of the vegetation provinces of the Pacific to the eighth Pacific Science Congress (Quezon City) (Fosberg 1957a). There were 21 Provinces defined for the Indo-Pacific Region including its continental margins. One of these was the Oceanic Province including all the true oceanic islands of the tropical Pacific except Hawaii and the Galapagos (in provinces of their own), and also excepting the atolls of Melanesia. Other provinces with which we will be working include the Papuan and Melanesian Provinces. A separate paper presented at the same congress described the vegetation of the Oceanic Province (Fosberg 1957b).

Curry-Lindahl's Zoogeographic Subregions of the Pacific Realm: In 1980, Kai Curry-Lindahl published a two part article in Environmental Conservation on the zoogeographically defined subregions of the Pacific realm. This paper had originally been presented to the 13th Pacific Science Congress (Vancouver 1975) and was apparently an attempt to refine Udvardy's biogeographic provinces in the region. Continental margins are excluded, but marginal archipelagos are not. Curry-Lindahl defines four regions (northern, western, central, and eastern) with the central region including five subregions (Hawaii, Micronesia, Melanesia, Polynesia, and Easter Island - Gomez).

Dahl's Pacific Biogeographic Provinces: In 1980, based on work ongoing for several years and with the support of the South Pacific Commission and IUCN, Arthur

Dahl published a Regional Ecosystems Survey of the South Pacific Area. The first part of the volume presents a breakdown of the insular Pacific into 20 biogeographic provinces. These tend to coincide almost exactly with archipelagos, and thus have considerable biological validity (as an artifact of dispersal and evolution), but they cannot reasonably be considered as ecosystems.

Dahl's biogeographic provinces were heavily influenced by the divisions of the three authors listed above and by Fosberg's "Biogeoclimatic Patterns in Micronesia" (13th Pacific Science Congress, Vancouver, unpublished) and G. Carleton Ray's "Preliminary Classification of Coastal and Marine Environments" (1975, since refined in Ray *et al.* 1984, Hayden *et al.* 1984). This last influence insures that Dahl's biogeographic provinces are not exclusively terrestrial.

Major Ecosystem Classification Units

The Biome: The largest widely accepted, definable terrestrial ecosystems are those to which the term "biome" is often applied. There does not seem to be much real agreement on defining this term or on either the breadth or degree of uniformity required in its components.

The biome concept was first proposed by animal ecologists (Kendeigh 1954; Odum 1945; Shelford 1913, 1932, 1963) as a major biotic community, but biomes are distinguished and recognized by their vegetation physiognomy. Whittaker (1962, p. 70) and Dahl (1980) even equate the term biome with formation. Whether or not a biome is necessarily a continuous area or can comprise all similar areas on a continent, or even in the world, is not agreed on. The term "major ecosystem type" has been used synonymously with biome. For the purpose of ecosystem classification, the following abstract concept seems most satisfactory: a biome is all members of a broad community complex marked by vegetation of similar physiognomy and with faunas adapted to the environment that supports and includes these vegetation types. This definition would place all temperate broadleaf deciduous forests in a single biome, or all coarse-leaved tropical grasslands and savannas, or all arctic tundra, or all mangrove swamps, or all cloud forests, or all montane-rain-forests. A biome is thus an ecosystem type. Probably any hierarchical classifications of ecosystems should have the biome or an equivalent concept as the highest level in its hierarchy.

Merriam's Life Zones: An alternative system might be life-zones, exemplified by the C. Hart Merriam scheme (Merriam 1898, also see Daubenmire 1938), eminently satisfactory for western North America, but difficult to use elsewhere.

Holdridge's Life Zones: Another life-zones scheme is the ingenious Holdridge scheme (1947, 1967), theoretically applicable everywhere, widely used in Latin America, but, strictly applied, requiring better climatic data than are usually available. In Latin

America, where such climatic data are generally lacking, Holdridge and his disciple, Tosi, have admitted to Fosberg that their recognition of these units is by the tree species known to be characteristic of the unit (also see Holdridge and Tosi 1972). Fosberg's experience with this scheme has been that where the required data are available, the vegetation is physiognomically about what is expected, except that transition types seem more prevalent than the main units. His scheme has not been widely accepted and may not be useful outside the northern neotropics, where it was developed.

Australian Land Systems: We must not neglect to mention, though briefly, the system of land survey and classification developed by C.S. Christian at the Australian CSIRO, and very widely used in Australia and New Guinea (e.g., Christian 1959, Christian and Stewart 1968). Survey teams of a botanist, a soils scientist, a geographer or climatologist, and others as needed, make a very broad field sampling of a large area. Their data are integrated into a landscape classification scheme of "land units" grouped together into "land systems."

All in all, the concept of biomes, as described in this section, seems the most satisfactory, in spite of the disagreement and confusion surrounding the term. The fact seems to be that confusion has grown up around every important synecological term. In general, the only safe way to insure understanding is for us to define our terms according to the way we use them.

Subsequent Ecosystem Classification Units

Formations: "Formation" is, at the same time, one of the most useful and definable, and yet one of the most variously misused and ambiguous terms in ecology. In geology it is used in a limited, well-defined sense, and also casually or colloquially for any feature that attracts attention. Both senses have their uses in facilitating communication.

In ecology there is no such agreement, but still, the term can be defined and the vegetation to which it is applied can be visualized. While it has generally been considered to apply to vegetation, it also may be useful in describing the vegetation component of an ecosystem. Restricted to its physiognomic, or more precisely, to its structural-functional sense (discussion below), it is essential in indicating and circumscribing major ecosystems at the next principal level below the biome. Vegetation composed of a majority of individuals with a given growth-form or category of growth-forms, in other words, a formation, is assumed to indicate the occurrence and circumscription of a definable major ecosystem with reasonably uniform components, at a rather broad level of generalization. Variations of this but not differing seriously may be called "subformations."

Dansereau (1958 pp. 17-27) has given us a useful essay toward a classification or grouping of vegetation formations, strictly on the basis of structure, the physical features of the plant aggregations. He sets up a series of ten "formation types" that are certainly logical and recognizable with familiar English word designations. From his discussion (p. 18) it seems that he regards these as "kinds of formations," but later on he seems to consider these also as formations per se.

He excluded the term "formation class" from this hierarchy and applied it to what he terms "regional climaxes," of which he enumerates and describes fifteen. These, though he refers to them as vegetation, seem, from his terminology, to include major environmental factors in their conceptualization. They correspond fairly well to the units which we call biomes, above, though they seem a bit broader than what are called biomes by some writers.

Fosberg (1961a, 1961c, 1967) adopted some of Dansereau's concepts, but modified his terms somewhat. Fosberg differentiated what Dansereau calls "structure" into two concepts, structure, involving spacing, stature, and stratification, and function, including morphological features of presumably adaptive significance - modifications such as thorniness, leaf reduction and texture, succulence, and the like. He kept the term "formation" in what seemed its traditional and most useful sense, a physiognomic unit more clearly defined by a combination of structural and functional features.

Higher levels into which the Fosberg formations fall are termed "great structural groups," based strictly on spacing, "formation classes," based mainly on stature, and "formation groups," rather than the more ambiguous "formation type," based on seasonality and deciduous or evergreen character.

It must be reemphasized that the IBP (Fosberg 1967) classification is strictly a vegetation system, artificial in nature, and deliberately avoiding implication of habitat, environment, or dynamics. These can be included, if needed, when the vegetation is used as an indicator of an ecosystem.

Associations: It is at the association level, however, that ecological and vegetation terminology have fallen into a hopeless semantic morass. "Association" as a term has been used at every level from the biome to the mini-stand. It has been defined in a plethora of ways. We would suggest that, as a vegetation term, association be limited to phytosociological use, for units determined by strictly prescribed methods in the Braun-Blanquet system and its modifications. This is its most widely accepted use and is well-understood in that sense. Ideally the term "association" should be discarded by other ecologists, or these workers should provide a definition when they use the term. Unfortunately, a new term for this level of description and classification is not readily available, so we recommend its use for the time being. For the purposes of an ecosystem classification, the term "association" or its alternative should be defined as a

recurring group of dominant or conspicuous organisms, plant and/or animal, inhabiting a recognizable and specific habitat type.

Other Infra-formation Categories: For the next level in our hierarchy, we are left without a formal category, and, indeed, perhaps without a set of comparable communities that may be logically grouped, at that level. On a regional basis, a consistent and comprehensive ecological classification is daunting. Island floras and faunas have, in their long histories diverged to such an extent that equivalence, from one to another, can no longer be established, except in an artificial fashion.

For our special purposes, on oceanic islands, there are not many biotic recurring equivalences, even at a generic level, that are convincing, though a few such can be pointed out, e.g., Metrosideros forests, Rhizophoraceae forests, Tournefortia scrub or forest, Scaevola scrub, Cyathea forests, sooty tern rookeries, Pisonia forests, Lepturus grassland and savanna, Miscanthus savanna, etc. More common, especially in uplands, are mixtures, but these merge into each other so as to be not easily classifiable. Classification is possible on an environmental basis using micro-climate, landform or physiography, available water, exposure, elevation, soils, rock-types, etc. Correlating these with biotic communities at this level may be possible, with adequate knowledge, but the result will be very diffuse. At low to moderate elevations the presence of exotic species complicates the situation enormously.

Our best suggestion is that below the association level, the difficulties be recognized, and local ad hoc arrangements and patterns of definable ecosystems be accepted. One example of an ad hoc classification at this level is that proposed by Gagne and Cuddihy for Hawaii (in Wagner *et al.* 1990 pp. 45-114). This is non-hierarchical classification at a very detailed level, indeed.

Another system, developed by the Natural Heritage Program of The Nature Conservancy of Hawaii, follows this ad hoc strategy at the fifth and sixth levels of a hierarchical system (Sam Gon, Ecologist, personal communication 1991). The Hawaii Natural Heritage system begins with a top level of "systems" (aquatic, subterranean, and terrestrial). The next level consists of six "elevation zones" (coastal, lowland, montane, subalpine, alpine, and multi-zonal), and the third level includes the three "moisture categories" (dry, mesic, and wet) defined on the basis of rainfall and drainage. The fourth level is based on "physiognomic categories" (desert, herbland, grassland, shrubland, forest, and mixed). The next two levels (community types and community subtypes) are defined by characteristic genera and species, respectively.

It will probably be felt that the suggestion of ad hoc arrangements for this level in the hierarchy is just the opposite of a classification, which is true. Some organization will probably be thought necessary. Stand types and landforms could be combined and arranged physiographically, if agreement could be reached as to what physiographic features are ecologically significant.

Another alternative is to group stand types by habitat. Habitat is an abstract concept consisting of one to many stands that are similar enough to be recognized and that are the living space for one or more conspicuous animals or plants. Of course, habitats exist for all organisms, but unless they are recognizable and definable, they can scarcely be classified in a useful way. Habitats of ecologically similar organisms (e.g., animal guilds) offer a possible basis for classification, but we have few conspicuous organisms in oceanic islands that occupy conspicuously distinctive situations. Habitats or habitat components (e.g., nesting or foraging habitats) for birds or fruit bats are possibilities. A necessity is that indicators of habitats are clear and conspicuous enough to be identifiable in the field. This limits habitat grouping to vegetation, soil, moisture or free water, or physiographic position.

Perhaps the most significant problem at the most detailed level of an ecosystem classification is a framework for the presentation of what we see at the stand level. Here is where the biodiversity is. At higher levels we merely talk about it. One cannot preserve a formation. One must preserve adequate stands within it. Therefore, our lowest level in the classification must be the stand or a group of mini-stands if these can be recognized.

Last Words on Classification Terms

For the purposes of ecosystem classification, criteria for distinguishing ecosystems requiring exacting, long-term, or detailed research should be avoided. The geographic facts of life - huge distances and the lack of easy access, and the resulting expenses - preclude the type of investigations on islands that are generally regarded as adequate for ecological science. For example, a classification that depends very heavily on soil or water chemistry (as with some of the systems we reviewed for wetlands and caves) will not work in the insular Pacific. For many of the most interesting islands, hit-and-run opportunities are the normal possibilities for exploration and investigation.

Finally, recognizability is the operating term. A theoretical classification, or many of them, can easily be constructed, but if their members cannot be described and recognized based on the descriptions, the system is no good. The boundary problem remains difficult, at whatever level we work in nature. Until we know what our lowest level (finest scale) ecosystems are and how to recognize their limits or boundaries, classification of the higher units is only an intellectual exercise.

A Selected List of References

Presented herewith is a list of references that anyone interested in ecosystem or vegetation classification on a world or Pacific island basis might find it profitable to read or scan. They are not selected to provide complete coverage of the field. Items on geographically localized areas outside the tropical Pacific are mostly omitted. Classification has been emphasized. Few items elaborating on the Braun-Blanquet system and the association concept are included. Items in English are emphasized.

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NEWS AND COMMENTS

40th Anniversary Reception

On November 24, 1992, the National Museum of Natural History celebrated the 40th anniversary of the Atoll Research Bulletin. A reception was held in the Director's Office to mark the occasion and to honor F. Raymond Fosberg, who launched the journal on September 10, 1951.

Since then, the Bulletin has put out 84 volumes containing more than 600 contributions. The Bulletin has also gained widespread recognition as a primary source of information on the biota, ecology, and geology of reefs and reef islands in the world's tropical oceans.



Director of NMNH, Frank Talbot joins Ray Fosberg with a group of his old colleagues. (Back Row L to R) Royce Oliver, Myron Winestein, Frank Talbot, and (Front Row L to R) Frank Whitmore, Josh Tracey, Ray Fosberg, and David Stoddart. (photo by Jane Beck)

Dr. Fosberg is a world authority on the botany and ecology of tropical islands, whose own publications have topped the 600 mark. Although he has been officially retired for thirteen years, he continues to conduct field research and to publish the results of his studies.

Each of the sixty guests at this gathering was asked to sign a copy of the 40th anniversary issue of the Atoll Research Bulletin, which was presented to Dr. Fosberg as a keepsake.



Josh Tracey, a contributor to the first issue of ARB, signs the 40th Anniversary issue as Ian Macintyre looks on. (photo by Jane Beck)



Frank Talbot presents Ray Fosberg with a signed copy of the 40th Anniversary issue of ARB. (photo by Jane Beck)

Book Notice

THE TURF ALGAL FLORA OF THE GREAT BARRIER REEF. PART I. RHODOPHYTA. Ian R. Price and Fiona J. Scott. James Cook University, Townsville, 1992. xii + 266 pp. (including 81 figs). Softcover.

Available from: The Bookshop, James Cook University, Townsville, Qld 4811, Australia [Phone (077) 814 812, Fax. (077) 251 209]. Price AUS\$61.95 (by surface mail within Australia or overseas). Cheques should be made payable to "James Cook University Bookshop". For credit card payment please specify whether Bankcard, MasterCard or Visa, give card number, expiry date and name of card-holder, and include your signature.

This volume deals with the turf-forming species of red algae occurring on the Great Barrier Reef. The publication provides detailed descriptions and illustrations of the 74 species recorded, with emphasis on vegetative features. In addition, data on nomenclature, type material, voucher specimens, habitat, seasonality and geographical distribution are given. Genus descriptions, keys to genera and species, a glossary and taxonomic index are also included. This is the first detailed treatment of the taxonomy and distribution of the turf algae which occur on coral reefs, where they are of major importance in trophodynamics. Although written for Australia's Great Barrier Reef, the work should prove useful throughout the tropical Indo-Pacific region.







ATOLL RESEARCH BULLETIN

NOS. 379-389

- NO. 379. MONSOONAL UPWELLING AND EPISODIC *ACANTHASTER* PREDATION AS PROBABLE CONTROLS OF CORAL REEF DISTRIBUTION AND COMMUNITY STRUCTURE IN OMAN, INDIAN OCEAN
BY PETER W. GLYNN
- NO. 380. CORAL REEFS OF THE SULTANATE OF OMAN
BY RODNEY V. SALM
- NO. 381. THE HETEROPTERA OF ALDABRA ATOLL AND NEARBY ISLANDS, WESTERN INDIAN OCEAN, PART 2. FRESHWATER HETEROPTERA (INSECTA): CORIXIDAE, NOTONECTIDAE, VELIIDAE, GERRIDAE, AND MESOVELIIDAE
BY DAN A. POLHEMUS
- NO. 382. STUDIES ON LITTORAL AND SUBLITTORAL MACROPHYTES AROUND THE MAURITIUS COAST
BY T. G. JAGTAP
- NO. 383. STUDIES ON THE BIOLOGY AND ECOLOGY OF THE INTERTIDAL ANIMALS OF THE CHICHIJIMA ISLAND IN THE OGASAWARA (BONIN) ISLANDS
BY AKIRA ASAKURA, SHIROU NISHIHAMA, AND YASUO KONDO
- NO. 384. PLANT COLONIZATION OF A RUBBLE BANK ON HERON ISLAND, GREAT BARRIER REEF, AUSTRALIA
BY R. W. ROGERS
- NO. 385. IMPACT OF TOURISM-RELATED FISHING ON *TRIDACNA MAXIMA* (MOLLUSCA, BIVALVIA) STOCKS IN BORA-BORA LAGOON (FRENCH POLYNESIA)
BY S. PLANES, C. CHAUVET, J. BALDWIN, J. BONVALLOT, Y. FONTAINE-VERNAUDON, C. GABRIE, P. HOLTHUS, C. PAYRI, AND R. GALZIN
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BY MARTIN L. H. THOMAS
- NO. 387. DISTRIBUTIONAL CONTROL OF SEAGRASSES BY LIGHT AVAILABILITY, TWIN CAYS, BELIZE, CENTRAL AMERICA
BY J. A. CALEM AND J. W. PIERCE
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BY DOUGLAS P. FENNER
- NO. 389. CLASSIFICATION OF NON-MARINE ECOSYSTEMS
BY F. RAYMOND FOSBERG AND SAM H. PEARSALL III

NEWS AND COMMENTS

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